Population processes in migratory birds

Papapavlou, Kelly

POPULATION PROCESSES IN MIGRATORY BIRDS

Kelly Papapavlou

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Chapter 1: THE SEARCH FOR POPULATION REGULATION IN MIGRATORY BIRDS

The concept of population limitation has occupied a central position in ecological studies for most of this century. Limitation is defined as the control of the abundance of a population, which is exerted as the combined effect of all the factors and all the processes that impinge on the population. This generalised definition presumes the existence of two basic mechanisms, the density-dependent and density-independent processes, the former regulating the population density, the latter acting independently of population numbers.

The identification and distinction between density-dependent and density-independent processes has been a difficult task for ecologists (see Chapter 2 , INTRODUCTION). Moreover, the subject of population regulation itself has generated a big controversy. Analytically, as far as the theory is concerned, the key properties of a population under regulation have been traditionally considered as follows (MURDOCH 1994):

- the population has an equilibrium density, derived as the result of feedback between the per head rate of change of the population and its previous density
- fluctuations in density are bounded, meaning that they change around an equilibrium level within limits.

However, it can be shown (MURDOCH 1994) that in certain cases (e.g. interactions between insect hosts and parasitoids), the feedback that gives rise to an equilibrium density can not account for a stabilising mechanism, so fluctuations in time are unbounded. Therefore, one of the conventional properties of population regulation, that of equilibrium density, is violated; equilibrium density may occur even in unregulated populations but only regulated populations show bounded fluctuations.

On the other hand, the concept of "equilibrium density" is also under debate. It has been proposed that the existence of regulatory mechanisms should not be anticipated in a non-equilibrial world (KREBS 1991). The argument against such a suggestion (GREENWOOD & BAILLIE 1991) is that a non-equilibrial world does not necessarily imply the lack of any regulatory processes; on the contrary, it may result from the occurence of delayed feedbacks, the interaction of several density-dependent processes and variation of the limiting factors.

In practical terms, population regulation has not been easy to verify. Mechanisms are often inadequately or incorrectly described, if described at all. The basic assumption that causes of death can be measured uniquely and attributed to a single factor may be fallacious, as mortality factors do not always operate independently or additively. Finally, statistical tests for density-dependence are often shown to lack credibility (BENSON 1973, KREBS 1991, MURDOCH 1994). Such facts , however, do not necessarily establish that population regulation mechanisms do not exist, but only that it is difficult to evaluate their action with certainty.

Birds, for example, comprise an animal group where the search for population regulation has led to opposing evidence. Birds counts are among the least variable of all year-to-year counts of animals, suggesting tight regulation. Mechanisms such as territoriality, that imply density-dependence, are common. Long-term time series data are available to analyse. However, most of the holistic approaches have failed to provide thorough evidence in favor of extensive density-dependence in bird populations (GREENWOOD & BAILLIE 1991, MURDOCH 1994). In contrast, isolated studies on certain species have established the importance of population regulation through food shortage affecting survival or reproduction (e.g. LACK 1966), parasites (MAY 1995), predators (e.g. KREBS 1970, EKMAN 1994, LINDSTROM et al. 1994) and social behaviour (e.g. ARCESE et al. 1992, SMITH 1994).

Population regulation in migratory birds forms a particularly intricate subject to study. Migratory species are inaccessible for half of the year; this fact complicates the estimation of population size and the correct neasurement and distinction between

mortality and emigration rates and recruitment amd immigration rates. Owing to distinct wintering and breeding grounds, it is very likely that processes that determine population numbers in one locality do not act correspondingly in another locality. Thus, what is defined as a limiting factor in one area does not inevitably play a significant role in another. Overall, accurate estimations of population parameters in migrant birds are problematic.

In spite of the difficulties, migrant birds comprise an extemely interesting subject of study provided that certain prerequisites are taken into consideration. Thus, it has been proposed (GOSS-CUSTARD 1993) that such migratory populations must be investigated at both local and larger scales: the local group is a manageable number of birds that has rather high rates of emigration and immigration and is usually studied at only one stage in the annual cycle. The larger population is studied throughout the year at a geographical scale at which there is effectively no emigration or immigration although much movement may occur between the local groups that it contains. Consequently, certain events are viewed differently according to the scale of the approach. For example, in studies at the breeding grounds, it is sufficient to know that there is competition for breeding space and that potential breeders are excluded. Because in most cases the "surplus" are males whereas it is females that determine the actual reproductive potential of the population, the size of the excluded "surplus" is less important than the fact that it exists. Yet when the subject of the study is the whole population, the word "surplus" is inappropriate as the birds contribute to the size of the larger population albeit that they do not breed. It is no longer adequate to disregard this group because, unless they all vanish, they will contribute to the pool of competing individuals, thus participating in the population processes.

In reality, the direct study of migrant species on more than one geographical scale may prove inefficient due to methodological and practical reasons. However, the quantitative formulation of models is helpful because it provides a means to understand how several quantities interact in complex systems. All model assumptions ought to be tested through monitoring and experimentation (GOSS-CUSTARD 1993). In addition,

migrant populations should not be seen as isolated from the community of which they are a part as there is evidence (HERRERA 1978) that migrant distribution patterns appear as community-specific ratios that do not depend to any extent on absolute abundances of individuals. Also, it should not be forgotten that certain characteristics of the life-cycle of migrants are not directly related to ecological processes but may be an outcome of physiological or genetic traits (e.g. the impetus to continue migration from a stopover site may not be a result of the effect of the habitat on the bird or of competition but of the "time-program" of the individual, BERTHOLD & TERRILL 1991). Last but not least, it should be remembered that some phenomena that do not occur in resident bird populations are of vital importance in migrant population dynamics (e.g. the return rate of migrants, ALBERICO et al. 1992, JENNI & JENNI-EIERMANN 1992, WILLIAMS & RODWELL 1992, ROTH & JOHNSON 1993, CUADRADO & HASSELQUIST 1994).

In this study I shall concentrate on long-term data from two migratory bird species, one passerine, the pied flycatcher (*Ficedula hypoleuca*) and one charadriid, the curlew (*Numenius arquata*). Flycatchers winter in Central Africa and breed in Europe; data are from a breeding population in southern England. The curlew population under focus consists of birds that winter at the river Tees estuary in northern England and breed in Fennoscandia (mainly Sweden and Finland). The purpose of the study was to test for evidence of population regulation in the pied flycatcher, particularly during the breeding season, and describe any possible general trends exhibited by the population. As far as the curlew is concerned, the aim was to investigate whether there is evidence that a ban of shooting during the years of the study led to any significant changes in the survival rates of curlews monitored at the Tees estuary. The influence of any alternative possible factors, other than shooting, was also examined

Chapter 2: THE CASE OF THE PIED FLYCATCHER Ficedula hypoleuca- IS THERE EVIDENCE FOR DENSITY-DEPENDENCE ? A FURTHER ANALYSIS

INTRODUCTION

Of major interest in population dynamics studies is to distinguish between density-dependent and density-independent processes and their relative importance in ecological systems. The former comprise factors that lead to a tendency for the death rate to escalate or the birth (or population growth) rate to decrease as the density of the population increases. The latter include parameters that influence the population size or structure itself in a way independent to the particular population density at any moment. Traditionally, it has been assumed that density-dependent factors have usually (but not always, see MAY 1974, 1975) a stronger stabilising effect than density-independent phenomena, which often include an element of stochasticity. However, it is sometimes difficult to distinguish between them as a random density-independent process would cancel itself out very quickly, thus leading to the same effect as a stabilising density-dependent factor (e.g. KREBS 1970). Moreover, the complexity of life-cycles themselves and the dynamic role of the species as parts of a community make even more intriguing the isolation and characterisation of certain parameters either as density- independent or as density-dependent. This task is absolutely essential for the elucidation of the way population size and structure is controlled.

Nowdays, it is emphasized (BEGON et al. 1990) that, although density-dependent processes are an absolute necessity as a means of regulating populations, their importance in determining abundance depends very much on the species and environment in question. Thus, a species' abundance reflects both density-dependent and density-independent factors, but, the relative importance and frequency of action of the two can greatly vary. As a result, species with comparatively extensive

geographical ranges are expected to provide adequate evidence for the changing relative importance of density-dependent/independent processes across the area they inhabit (ENRIGHT 1976). Such organisms are assumed to be under density-dependent regulation at the core of their range where the environmental conditions are more favourable, whereas in marginal areas their population density is apparently limited by the physical environment (e.g. JARVINEN 1980). Overall, this theory predicts that the intensity and nature of density-dependent and density-independent factors will vary along the geographical range of a comparatively widespread species.

The pied flycatcher *(Ficedula hypoleuca*) is a migrant passerine whose breeding range extends from Central Africa (ISENMANN & MOALI 1987) to Western and Central Europe (LACK 1966, HARVEY et al 1984, POTTI & MONTALVO 1991), Estonia (VILBASTE & LEIVITS 1987) and Fennoscandia (including Lapland) (ALATALO & LUNDBERG 1984, JARVINEN 1980, NYHOLM 1986). Several studies have examined the possible factors that act on its population size, either of density-dependent or of density-independent nature (BAILLIE & PEACH 1992). In this chapter, I will focus on an extended set of data from the pied flycatcher population of the Forest of Dean, Gloustershire, U.K. A previous study undertaken in the same area and on the same population (STENNING et al. 1988) has provided some evidence on density-dependent regulation at some stages of the study. Thus, STENNING et al. (1988) supported that:

- during the first 7 years of their study, high breeding population densities were associated with small clutch size
- mortality in the nest showed no evidence of being related to population density
- mortality (and emmigration) of breeding birds in the study area outside the breeding season was highly correlated with total post-fledging density

In this chapter, I will explore whether 4-years additional data change the overall view on pied flycatcher population dynamics presented by STENNING et al (1988). I will also try to check whether any general trend might be detected in this population.

MATERIALS AND METHODS

the species:the first male pied flycatchers arrive in England from Africa during April about 10 days before the first females (STENNING et al. 1988). They then choose a hole which they defend as the centre of their territory at which they display after the females arrive. They readily take to artificial nest boxes as the scarcity of natural cavities seems to be a limiting factor for their geographical distribution and density in the wild (LACK 1966, JARVINEN 1980, NILSSON 1984). A small proportion of males are polygynous but, unlike the majority of other polygynous bird species, they do not defend an extended territory where more than a single female nest. As males do not often provide any help to the secondary female towards the establishment of her brood, it is not known why some females end up with mated males; have they been decieved (deception hypothesis) or is their choice a trade-off (polygyny threshold hypothesis) between the possibility of staying unmated and the consequent decrease of their fitness by raising alone a whole brood ? (ALATALO et al. 1981, SLAGSVOLD & DALE 1994). The primary female might also mate with other males during the absence of the primary male. A great percentage (39.7% for males and 40% for females) which is mostly comprised of young (1st-year-old) birds remains unmated each year (LACK 1966, HARVEY et al. 1985). This percentage appears to be higher in other studies (up to 70%, NYHOLM 1986, POTTI & MONTALVO 1991) although this may also be a sampling bias as mated males are often difficult to catch and mark. The reasons for postponing breeding are vague ; it seems that some pied flycatchers do not breed in their first year even in the absence of limitation of breeding holes or mates (HARVEY et al. 1985, POTTI & MONTALVO 1991).

During the egg-laying period, one egg is usually laid per day although there have been variations to this rule mainly caused by extreme weather conditions (PULLIAINEN et al 1994). Incubation lasts for approximately 15 days (during which

the primary female is fed by the primary male), so does the period between hatching and fledging (STENNING et al. 1988). The return rate of the birds is very low (STENNING et al. 1988), the highest reported from other studies being 15.8% (NYHOLM 1986, POTTI & MONTALVO 1991)

the habitat: the data were collected from 1948 to 1969(spring) in the Forest of Dean, Gloucestershire, U.K. which belongs to a 140-year-old oak plantation (*Quercus robur).* A part of this area has been grazed. Pied flycatchers nested in artificial nestboxes first placed ther in 1942. The number of nestboxes has always been much in excess of the maximum number of the pied flycatchers pairs in the area, reaching up to 339 boxes. To avoid bias due to microhabitat differences (NILSSON 1984) only broods in nest-boxes were considered excluding the ones (very few) in natural cavities. Birds were ringed as nestlings or as breeding adults, the female and males were caught while incubating or feeding the young. Each nestbox was checked during the breeding season every few days from 1948 to 1964 and every day from 1965 to 1968 inclusive. Thus, the four last years of the study were the most intensive ones. The data used for years 1948-1964 were derived from table 1 (STENNING et al 1988). The whole data set of the twenty-one breeding seasons (1948-1968) is shown in appendix I.

the analysis: the method employed is the key-factor analysis as first described in VARLEY & GRADWELL (1960). It is applied to a series of successive life-table stages where each k-value is calculated as the logarithm of the population size entering the specific life stage minus the logarithm of the population size at the end of the same life stage, that is

$$k=\log [Di/Di+1]$$

where i=life stage at t and i+1= next life stage at t= i+1

It is obvious that as the ratio Di/Di+1 increases, so does the k-value. If the difference between Di and Di+1 represents losses due to mortality, then the k-value is an index of the intensity of mortality at each life stage. On the other hand, if the difference between Di and Di+1 is a result of animals achieving less than the maximum of possible

natality, then the k-value stands for the relative decrease in the potential natality of the population. All k-values derived for each stage are summed to give the total mortality $K\tau$ of the year and plotted against time to assess its relative importance as compared with the $K\tau$ value. Relationships between individual K-values and environmental variables may solve the ambiguity of the parameter that causes the mortality in a particular life stage. Regressions between the Ki value in a series of years and the logarithm of the initial population on which it acts can provide evidence for density-dependence, if the larger the initial population is the stronger the mortality factor appears to be.

The main advantages of the key-factor analysis are that:

- it permits an immediate understanding of the way populations vary in time as the K τ gives a realistic view of the total mortality suffered by the population during a numbers of years.
- it allows a definitive assessment of the relative intensity of each parameter acting on the population, plus, its temporal consideration provided that the life-cycle stages of the species are correctly judged and the events that have an influence on population size are properly defined
- it facilitates the investigation of the role of natality in population dynamics
- it helps the qualitative comparisons with similar patterns exhibited by other species (SOUTHERN 1970)
- it enables the distinction between different ways of operation of density-dependence e.g.direct or delayed density-dependence, overcompensation, undercompensation (SOUTHWOOD 1966, BEGON et al. 1990)

The disadvantages of key-factor analysis are primarily of statistical nature. As most of the procedures that employ regression

- it is very sensitive to sampling errors (SOUTHERN 1966, KREBS 1970, ITO 1972)
- it is prone to interpretation bias of the correlation results. This means that even if there is a statistically significant relationship between factors A and B, this does not

imply that, in biological terms, there is also causal connection between them (PETERS 1991). For example, if in reality factor A is related to a (sometimes unknown) factor C and factor B is also related to the same factor C, then, a correlation between A and B will prove to be statistically significant despite the lack of actual connection within them. Moreover, even if A and B are shown to be directly related, it is often hard to decide on which one is the cause and which one is the effect.

- there must be assumed constant residual variance and normality for the dependent value (CAMPBELL 1989).

For the purpose of the comparisons, k-values were calculated as in STENNING et al. (1988) :

- k1=log[(max. clutch size +2)*N/(aver. clutch size +2)*N]
- k2=log[(aver.clutch size +2)*N/(aver.hatch.numbers +2)*N]
- k3=log[(aver.hatch.numbers+2)*N/(aver.fledg.numbers+2)*N]
- k4=log[summer population in year t/breeding population in year t+1]

For years 1948-1964, N is the number of broods as defined by STENNING et al (1988), that is those produced within 7 days before or after the mean laying date. However, for years 1965-1968, I calculated two different series of data, one where N was defined as in STENNING et al. (1988) and another where N represented the broods produced within 7 days before or after the modal laying date instead of the mean. Considering that the mode is a biologically more meaningful term as it represents the birds' preferred date of laying initiation and taking into account that breeding success is often related to the date of first egg laying (LACK 1966, JARVINEN 1980, 1982, 1989, 1993, JARVINEN & VAISANEN 1984 but JARVINEN & VAISANEN 1989), it would be interesting to see if such a differentiation will lead to statistically significant results in overall k-values. In each case, normal broods are called only the broods produced 7 days before or after the mean (or modal) laying date respectively. Therefore, this number underestimates the

total number of broods actually produced. The mean laying date data include a higher number of late broods:

Table 2.1 : First egg laying dates of pied flycatcher clutches,Forest of Dean, 1965-1968

(May)	1965	$N_{(1965)}$	1966	$N_{(1966)}$	1967	$N_{(1967)}$	1968	$N_{(1968)}$
MEAN	16.57	54	14.8	56	14.71	58	16.37	49
MODE	15	55	9	47	14	58	15	50
MEDIAN	15	-	13.5	-	14	-	13	-

In all cases, N is considered constant during the whole breeding season, that is the death of adult birds is considered negligible. N is only calculated for the normal broods, so the actual number of breeding birds might be underestimated. The maximum clutch size ever observed is ten (STENNING et al. 1988), thus, it is also presumed to be the maximum potential one.Also, polygyny is considered insignificant, that is each brood is thought of consisting of one a-male and one a-female.

k1 includes all the factors that might lead to a decreased number of eggs being layed, therefore, it is more an index of less than optimal natality than direct mortality. k2 incorporates factors related to all forms of mortality between laying and hatching, such as predation, improper incubation, egg robbery, deserting of the clutch or incomplete embryo development (YLIMAUNU & JARVINEN 1987, JARVINEN & VAISANEN 1989, HALLSTROM & OLSSON 1994, SIIKAMAKI 1995 and personal data). k3 is mortality between hatching and fledging, mainly owing to predation, inherent weakness of the juveniles or starvation. The initial population in k4 consists of all adults and fledglings produced during the breeding season of the year including the ones developed from a "non-normal" brood. Thus, the initial population in k4 does not have to coincide with the final population in k3 as it comprises the total summer population. As a k-value, k4 embodies mortality during migration to and from the wintering grounds, immediate post-fledging mortality, casualties at the wintering area and losses due to emigration. As a result, it is only conventionally defined as a mortality factor as

it definitely comprises birds that have disappeared from the study area but are still alive.

RESULTS

The general trend in the changes of k-values over time does not alter from what was presented in STENNING et al (1988): it is evident that K4 is the fundamental factor determining the degree of mortality during the twenty-one breeding seasons. Not only does K4 affect the number of breeding birds each year, it also regulates the temporal variation in population density (K4 correlates with $K\tau$, r:0.853, b:0.924, n:19). The "mode" and "mean" distinction for the 1965-1968 data does not lead to any conspicuous variations (figures 3.1A-3.1B).It is of interest that at least visually the k1, k2 and k3 values do not seem to differentiate substantially during the twenty-years period (this has not been statistically tested though). This implies that the absolute clutch size, number of hatchlings and number of fledglings remained relatively constant during the study period ; however, STENNING et al. (1988) reported that k1 statistically increased during the 17 years of their study.

Figure 2.1A (modal laying date): Changes in k-values over time

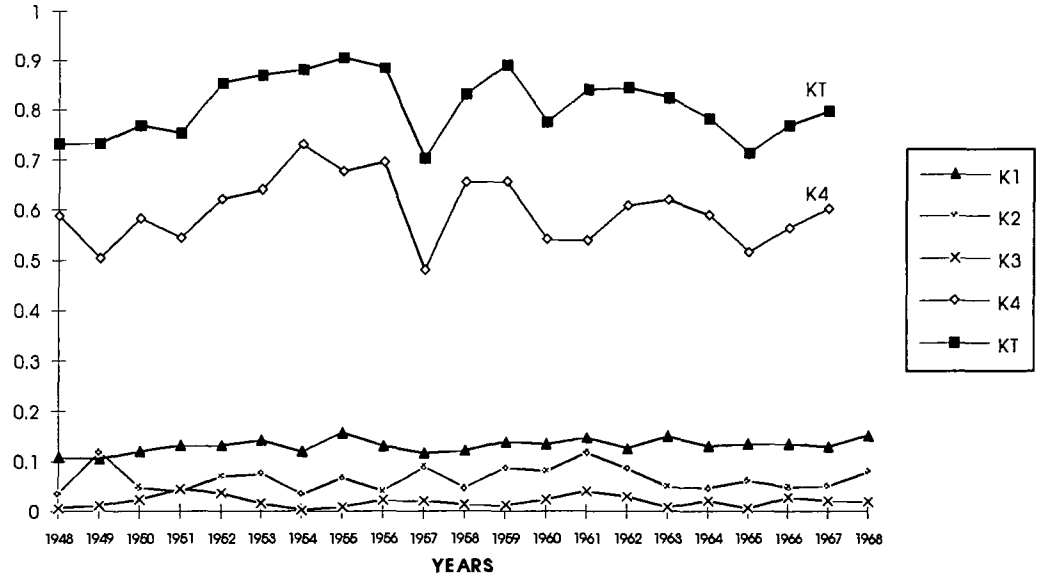
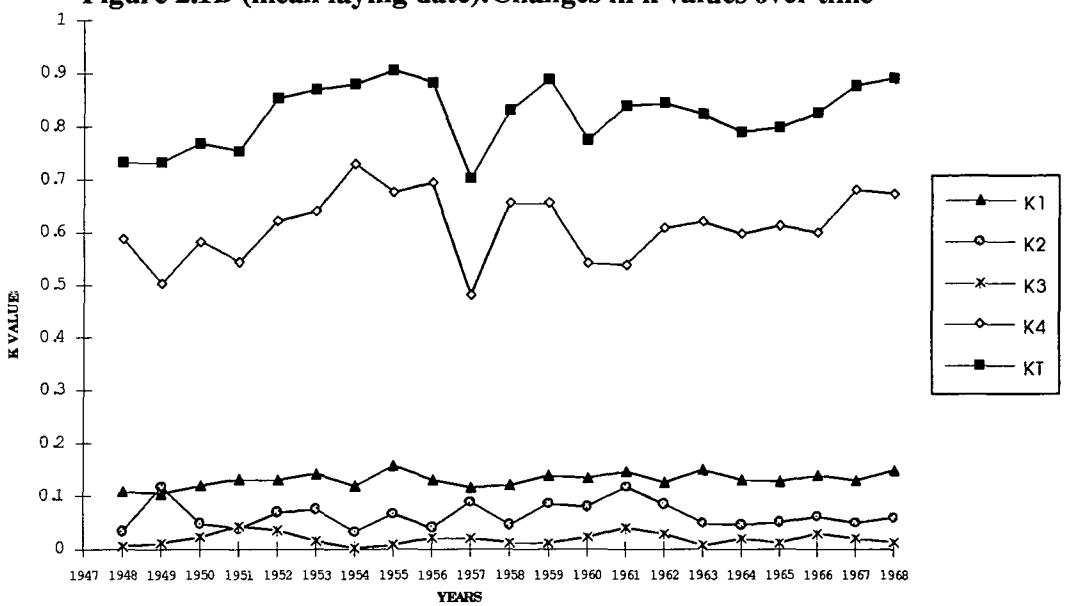


Figure 2.1B (mean laying date):Changes in k-values over time



Following the scheme employed by STENNING et al (1988), density-dependence was tested in four consequent phases:years were grouped so that each value was separately regressed for 1948-1954, 1955-1964, 1965-1968 and 1948-1968.The 1965-1968 group includes the new data gathered during the last, intensive part of the study. As it is evident from graphs 2, 3, 4 and 5 , in no case did the overall K-value (1948-1968) show a statistically significant correlation with the logarithm of the previous density. This trend did not change despite the introduction of the extra data and the

modification according to the mode, instead of the mean, laying date (table 2.2A-2.2B).

Table 2.2A (modal laying date): Regression coefficients for individual k-values plotted against the log (population size immediately before mortality acts)

	1948-1954 (n=7)	1955-1964(n=10)	1965-1968(n=4)	1948-1968(n=21)
k1	r=0.7874 * b=0.134, p=0.029	r=0.3293 b=0.0927	r=0.5243 b=0.12	r=0.1214 b=-0.01
k2	r=0.7142 b=0.0316	r=0.0614 b=0.035	r=0.3006 b=-0.0931	r=0.0795 b=-0.0216
k3	r=0.7891 * b=0.1665, p=0.028	r=0.4135 b=-0.085	r=0.3741 b=-0.0743	r=0.1595 b=0.0191
k4	r=0.3193 b=0.434	r=0.7454 * b=0.988, p=0.001	r=0.8548 b=-0.0337	r=0.2019 b=0.182

Table 2.2B (mean laying date) :Regression coefficients for individual k-values plotted against the log (population size immediately before mortality acts)

	1948-1954(n=7)	1955-1964(n=10)	1965-1968(n=4)	1948-1968(n=21)
k1	as in table 2A	as in table 2A	r=0.7632 b=-0.24	r=0.098 b=0.0156
k2	"	"	r=0.4898 b=0.074	r=0.0644 b=-0.018
k3	"	"	r=0.3401 b=0.065	r=0.1994 b=0.024
k4	"	r=0.7413 * b=0.9801, p=0.012	r=0.353 b=0.6025	r=0.19 b=0.163

*:p≤0.05

Figure 2.2A(modal laying date): Regressions of k1 values against the log of the previous density

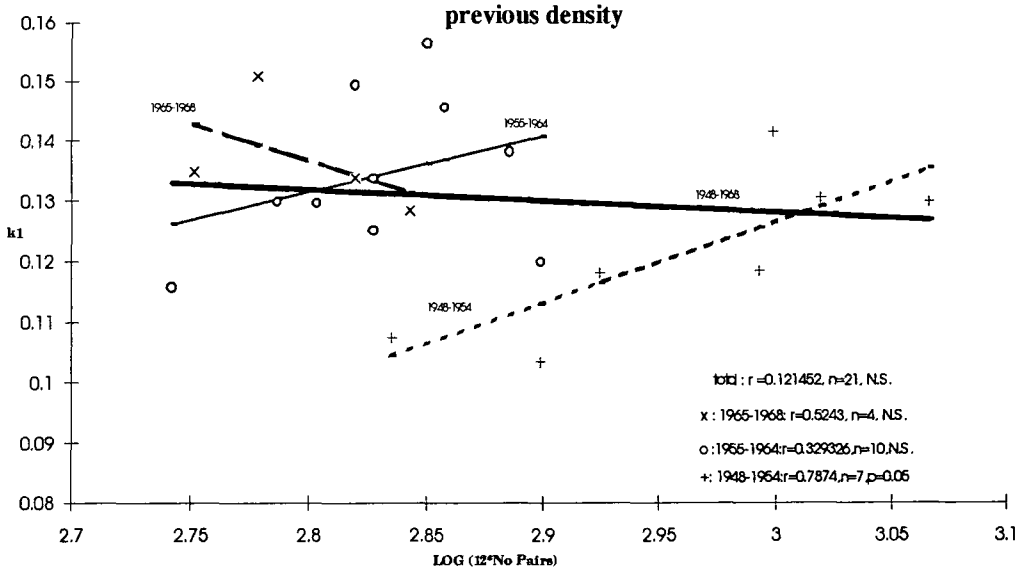


Figure 2.2B (mean laying date) : Regressions of k1 values against the log of the previous density

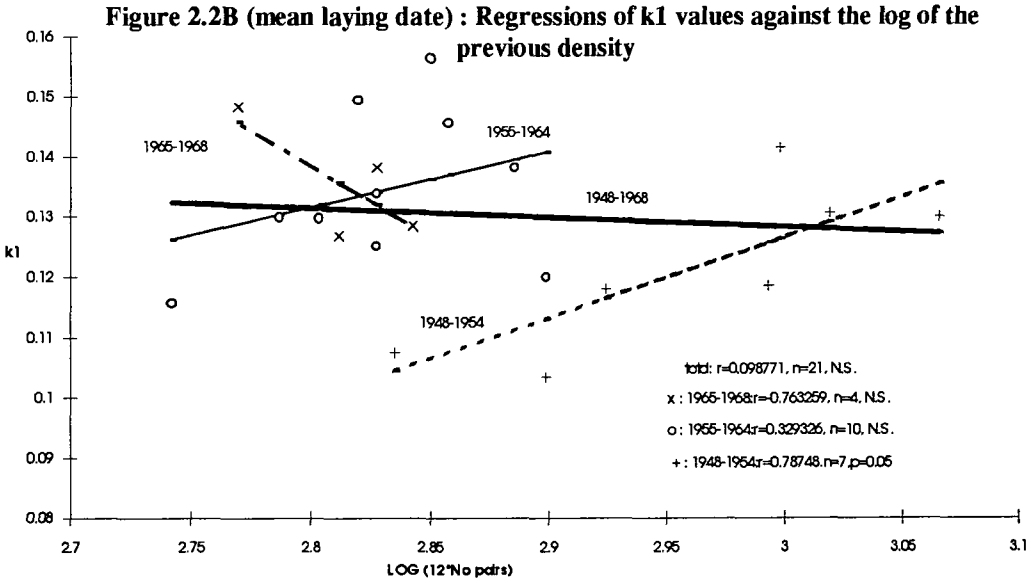


Figure 2.3A (modal laying date): Regressions of k2 values against the log of the previous density

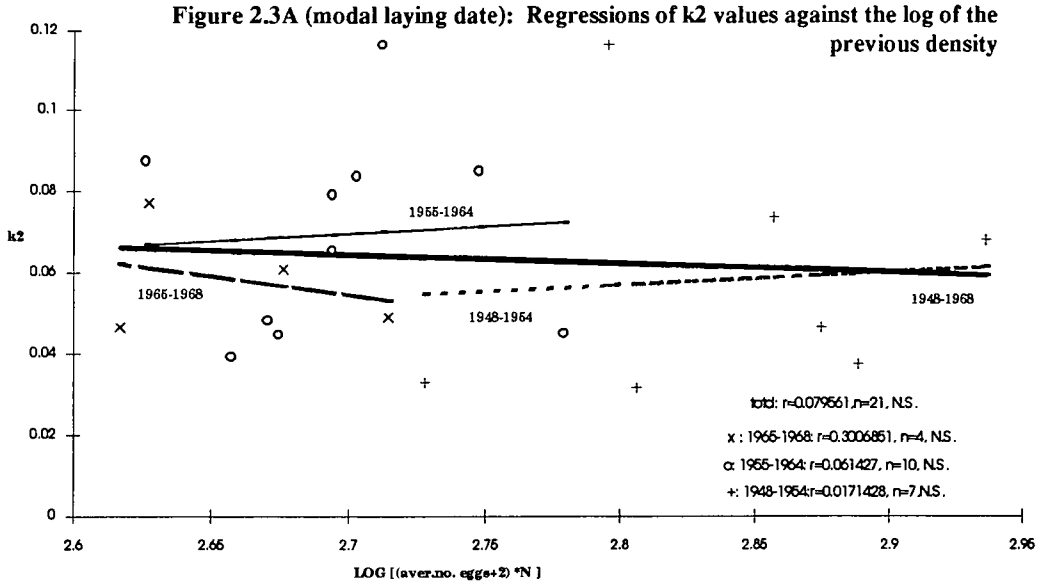


Figure 2.3B(mean laying date):Regressions of k2 values against the log of the previous density

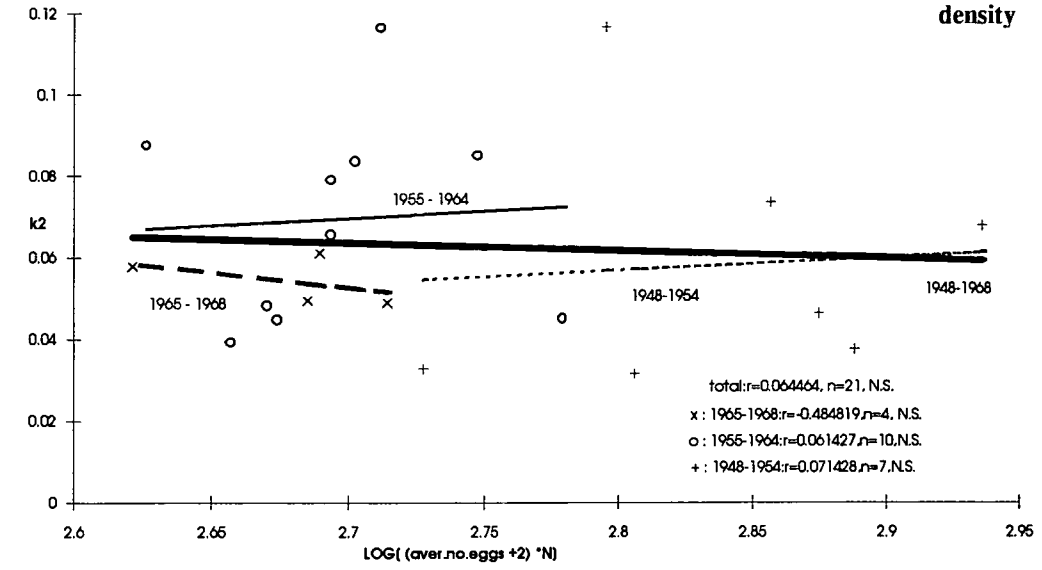


Figure 2.4A(modal laying date): Regressions of k3 values against the log of the previous density

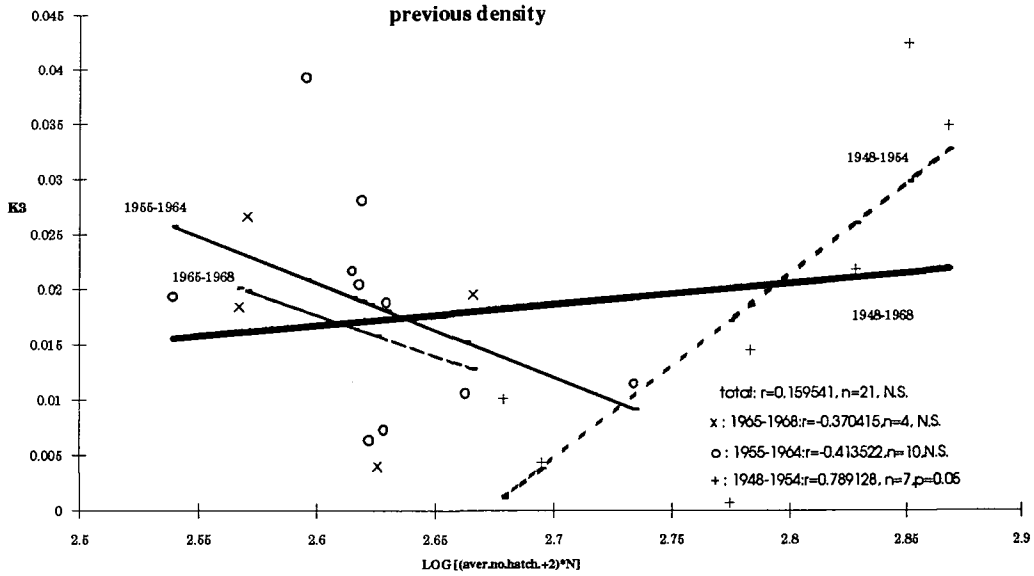


Figure 2.4B (mean laying date): Regressions of K3 values against the log of the previous density

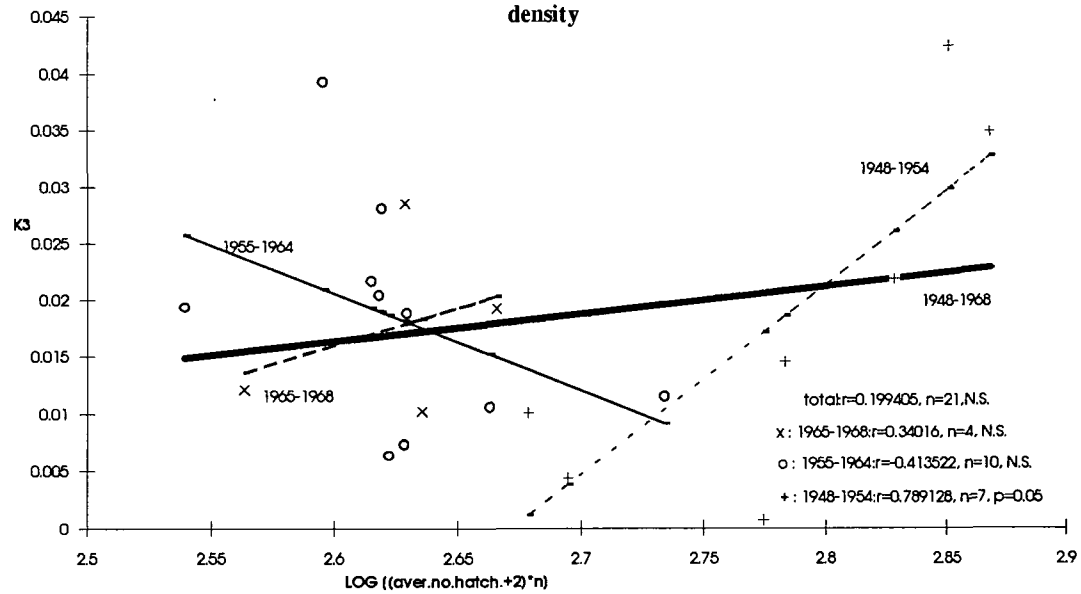


Figure 2.5A (modal laying date): Regressions of k4 values against the log of the previous density

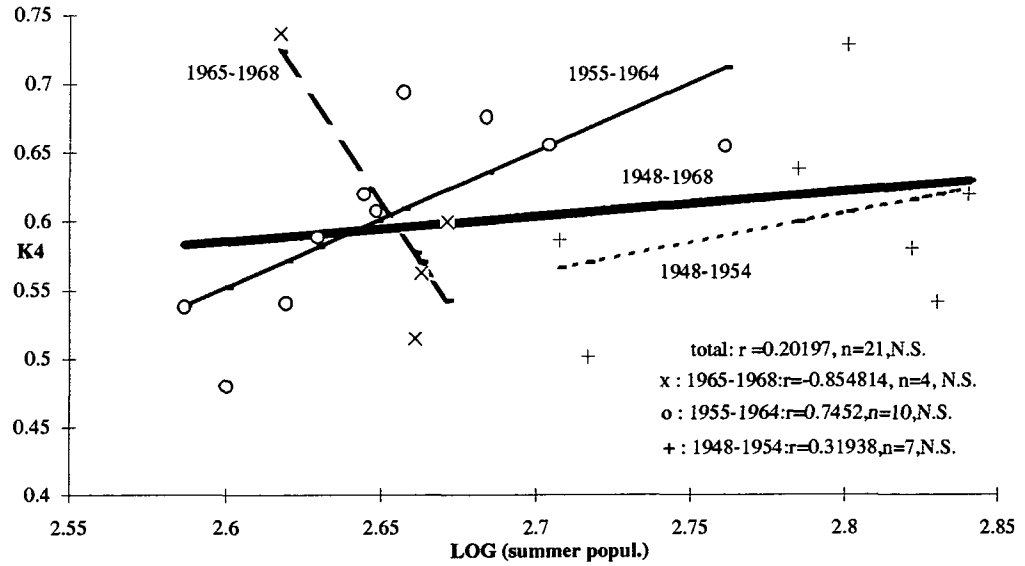
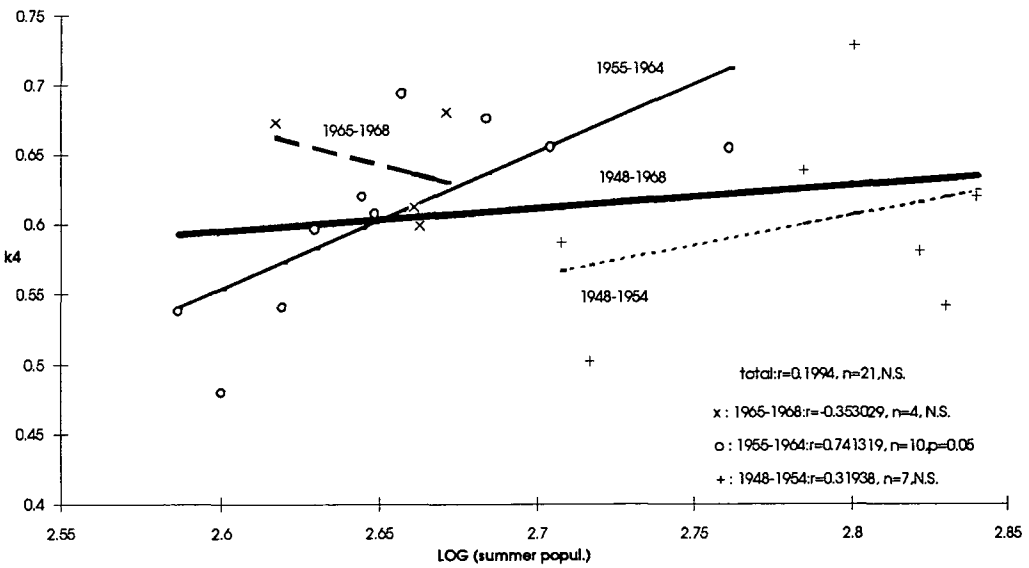


Figure 2.5B (mean laying date): Regressions of k4 values against the log of the previous density



A further look at each k-value separately reveals that , for the years 1948-1954, k1 shows a statistically significant correlation (Figure 2.2) with the logarithm of the maximum potential population size (D1=12*N). In reality, k1 is regressed against the number of pairs laying normal broods as this number constitutes the parameter that varies among the years .In this case, the evidence for density-dependence is that k1

(1948-1954), indicating depression in fecundity,increased in relation to the population size at the beginning of each breeding season. In the same time period, k3,which represents losses between the hatching and the fledging stage, is also regressed in a statistically significant way on the number of hatchlings (Figure 2.4). The evidence is, therefore, that the mortality during the fledging stage in years 1948-1954 may be density-dependent. Last, k4 in the years 1955-1964 appears to correlate in a statistically significant way with the logarithm of the total population size at the end of the summer.

The "mean" and "mode" correlation coefficients for the 1965-1968 period are not statistically significant and do not alter dramatically the overall impression about the respective k-value. However, it is interesting that the regression lines for k3-values in years 1965-1968 are of opposite sign (negative for the "modal laying date" data, positive for the "mean laying date" data).There is a high possibility that this represents a statistical error as the residuals for the 1965-1968 data were not normally distributed.On the other hand, it may be observed that the k3-values themselves are very similar (appendix I) but, from figure 2.4A, it can be deduced that the "mortality factor" in 1966 acted on a much smaller population of hatclings , thus placing the k3-value towards the left of the diagram. This could be an indication that the "mortality factor" acted with the same intensity on two populations of remarkably different size. This probably relates to the number of broods taken into account for 1966 which was considerably different for the mode and mean laying date data respectively. Is this an indication of how likely it is to get highly deviating results because of selecting a dissimilar starting point?

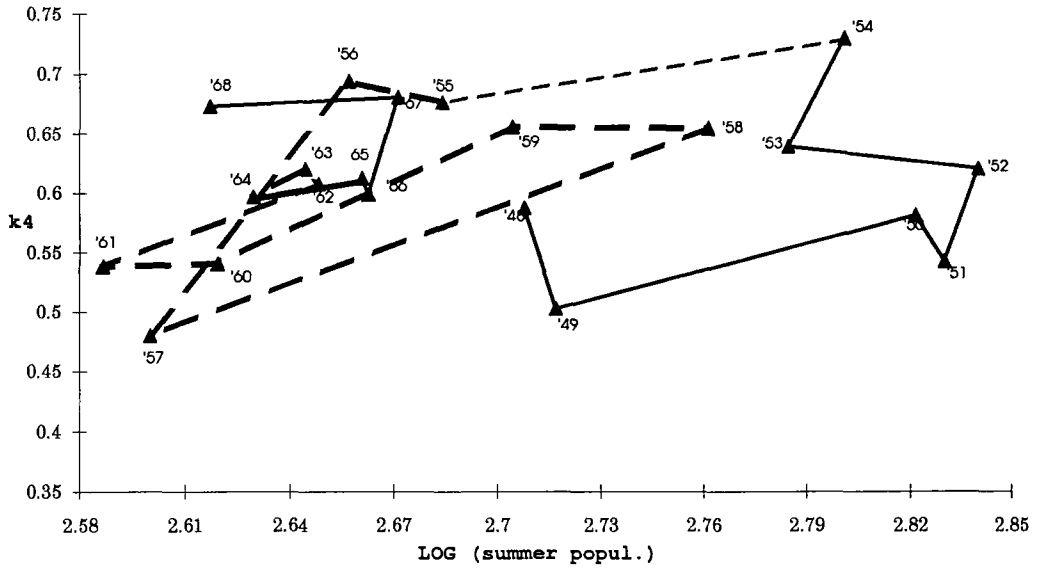
DISCUSSION

Summarising the conclusions from the density-dependence analysis, it becomes quite clear that, at first sight, population regulation does not seem to occur to a great extent in the Forest of Dean pied flycatcher population. No k-value showed a significant trend in relation to population size at the beginning of the respective life

cycle stage. There is only limited evidence for density-dependence during particular time periods and for certain k-values [k1(1948-1954), k3(1948-1954), K4(1955-1964)]. The results agree with two other studies (VIROLAINEN 1984, JARVINEN1987) which report lack of direct density-dependence in two breeding flycatcher populations from the South and the North of Finland respectively. (However, in JARVINEN 1987 there is evidence for density-dependence outside the breeding season.) In both studies K4 comprises the key-factor.

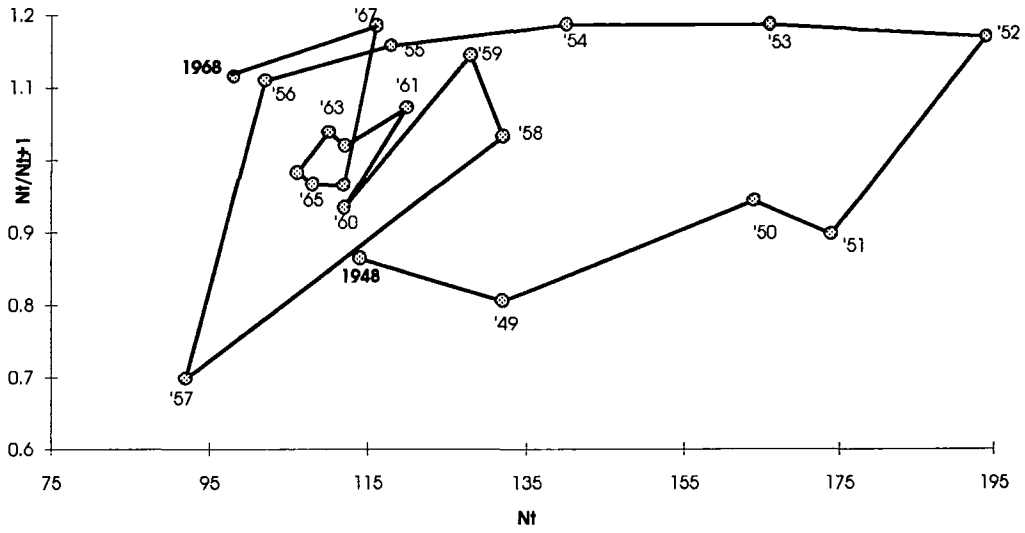
This particular pied flycatcher population exhibits a very interesting cyclic pattern when the K4 values are plotted against the logarithm of the summer population (STENNING et al. 1988). I reproduced the same pattern using all K4 values available including the ones from the period 1965-1968 (mean laying date data). From Figure 2.6 it can be deduced that the same motif persists in years 1965-1968 giving rise to another cycle.

Figure 2.6: A possible cyclic pattern in 20 years of mortality in the pied flycatcher



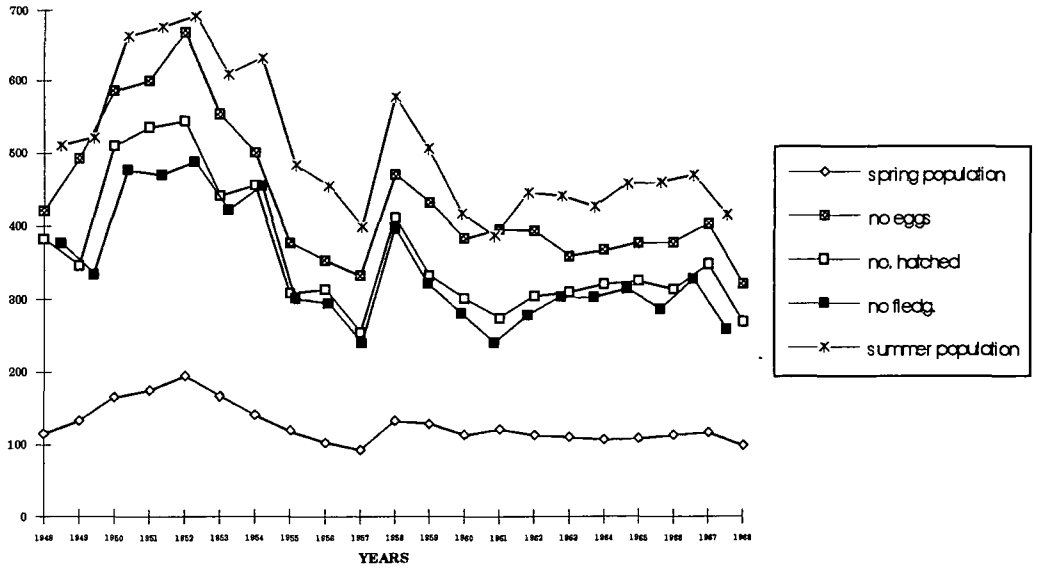
In order to try to interpret it, I plotted (Figure 2.7) the degree of population change from one generation to the other (Nt/Nt+1) against the initial population Nt (Nt= number of breeding individuals in spring, that is normal broods*2). Thus, the point numbered as "1948" depicts the relative change of population size between years 1948-1949 (N_{1948} /N_{1949}) against the population size in 1948. If all the points for successive years are joined as in Figure 2.6 another cyclic pattern is revealed.

Figure 2.7: Cyclic fluctuations in breeding population size



The sequence of the values in Figure 2.7 seems to imply a particular trend. From 1948 to 1951 Nt/Nt+1 < 1 although Nt increases, This means that in absolute numbers the population size as defined by the number of pairs forming normal broods in spring increases.This trend is also evident in Figure 2.8 From 1952 to 1956, Nt/Nt+1>1, that is the population size decrease (Figure 2.7, 2.8). From 1956 to 1957, the ratio changes from >1 to <1, an indication that in 1957 the breeding population size increases again. Years 1958 to 1966 have a relatively steady Nt/Nt+1 which roughly equals 1. In year 1967 the spring population size starts decreasing again, so does in 1968.

Figure 2.8:Temporal changes in population parameters



Turning to Figure 2.6, it can be seen that the trend that K4 follows, corresponds to the spring population size trend: from 1948 to 1951, when the population size increases in approximately constant rate, K4 remains steady and at comparatively low levels. In 1952 it increases whereas Nt decreases and in 1957 it drops again when the number of breeders increases.From 1958 to 1966 it fluctuates only a little bit whereas it appears remarkably higher in 1967 and 1968.

If data from VIROLAINEN 1984 are analysed in the same way, a similar pattern appears (Figure 2.9, 2.10). K4 shows cyclic fluctuations which appear as a spiral, anti-clockwise motif (a result of the remarkable population decline in time, see VIROLAINEN 1984). In contrast, data from JARVINEN 1987 give rise to random fluctuations (Figures 2.11, 2.12).

Figure 2.9: Spiral changes in a population of pied flycatchers in southern Finland

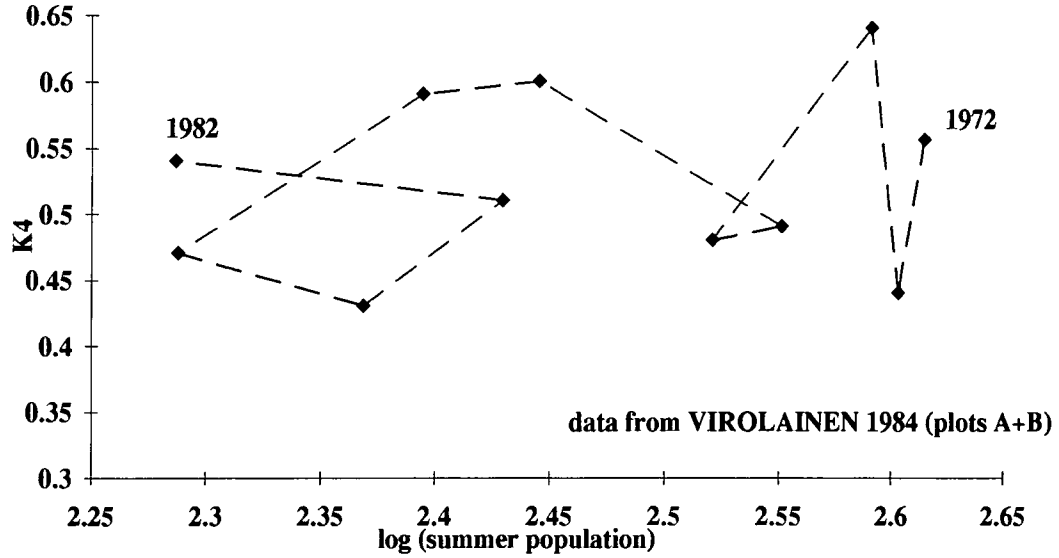


Figure 2.10: Spiral changes in breeding population size

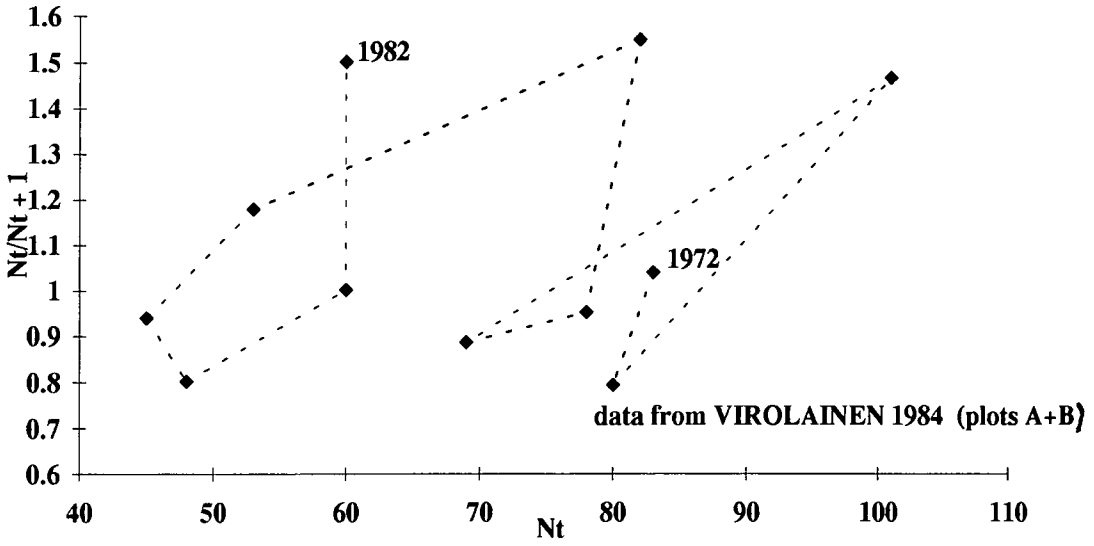


Figure 2.11: Random fluctuations in a population of pied flycatchers in Lapland

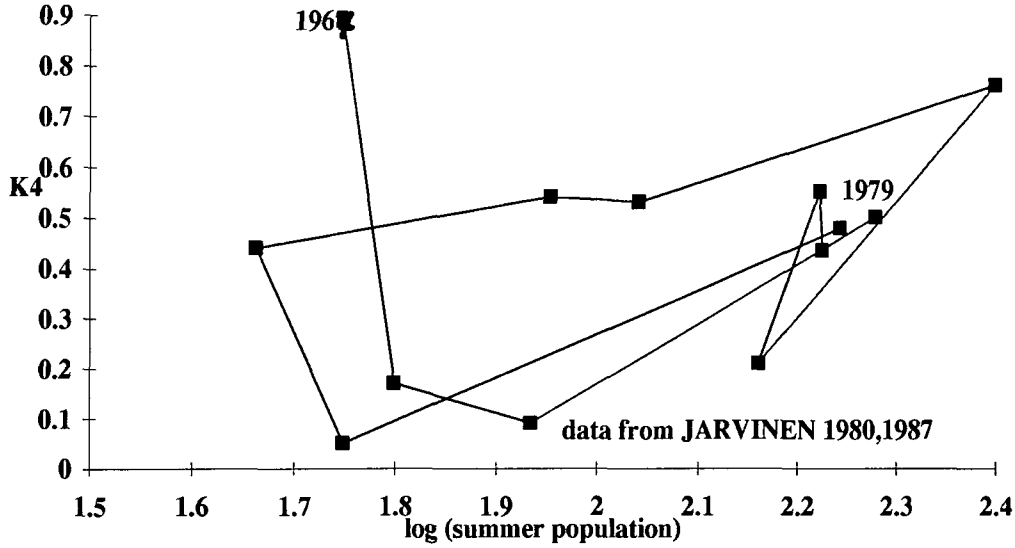
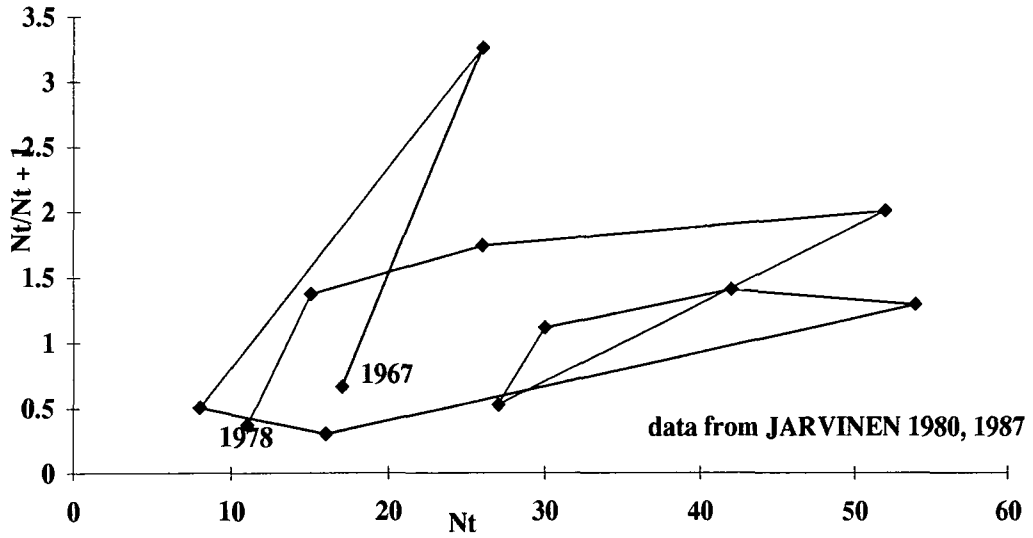


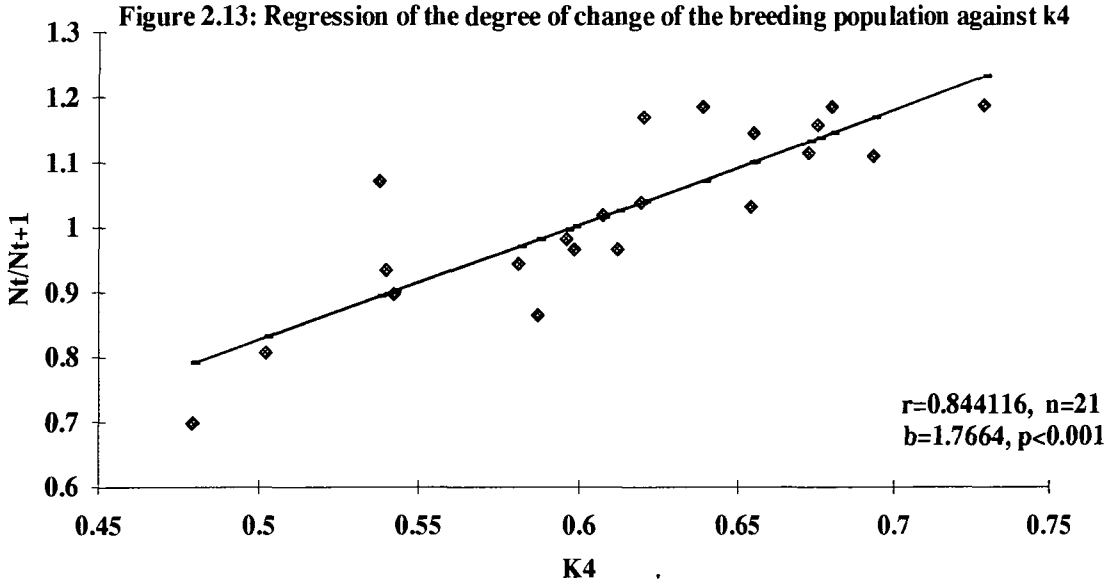
Figure 2.12: Random fluctuations in breeding population size



In conclusion, it seems that regulation in the pied flycatcher population in the Forest of Dean takes place at the level of the breeding birgs each year. This process is reflected on the value of the K4 which is the key-factor in determining the population fluctuations from year to year. It can be deduced that K4 signifies a trend in the

population of breeders (Nt) and not in the population size overall. When Nt increases K4 values are relatively low and when it decreases they are high. Indeed, the K4 values and the corresponding changes in the numbers of breeding pairs from spring to spring are highly correlated (Figure 2.13).

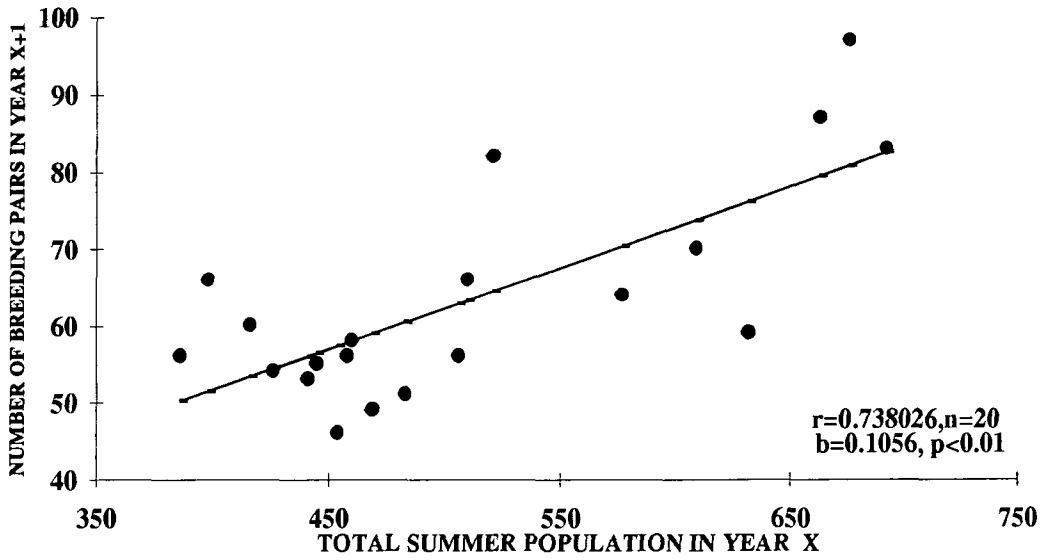
Figure 2.13: Regression of the degree of change of the breeding population against k4



The fact that K4 has probably nothing to do with the size of the summer population can be derived from Figure 2.5 : K4 shows no significant correlation with the logarithm of the summer population size. However, it may be argued that K4 in years 1955-1964 does show a statistically significant correlation with the previous density. I think that this is an artificial result owing to the way points for the respective years are located in the cyclic pattern in Figure 2.6 . It is also true that the regression of the number of breeding pairs in year x+1 against the total population size in summer is highly significant (Figure 2.14) However, I believe that this is again an artifact of the analysis and the population processes themselves; numbers of fledglings correlate very well with numbers of hatchlings, eggs and clutches. This can be visualised in Figure 2.8 although it is also shown statistically in appendix I. Thus, a high summer population is usually the result of a high number of broods, that is a large spring population size. A

high population size in summer is the result of a high population size in spring but not the immediate cause of it. If it were , it would have been correlated significantly with at least one of the groups that form breeding pairs in the spring population (immigrants, natives, residents) but it has not (STENNING et al. 1988).Even if the trend has a biological explanation (i.e. the more successful reproductive performance, the more birds return to breed next year), its effect must be usually masked by other phenomena

Figure 2.14: Regression of the number of breeding pairs on the size of the population at the end of the previous summer



What might be the possible biological mechanism that evokes this cyclical pattern in K4 and the size of the spring population of pied flycatchers in the Forest of Dean? Predation is considered as one of the most well-supported factors giving rise to dumped oscillations in populations (BEGON et al. 1990). However, a predator acting only in a particular life-cycle stage of the pied flycatcher (that of the k4) is not known. The only cases of predation reported are during the nesting period , thus, influencing other mortality factors and not k4 (YLIMAUNU & JARVINEN 1987, JARVINEN & VAISANEN 1989, HALLSTROM & OLSSON 1994, SIIKAMAKI 1995 and personal data). Parasitism is also referred as a powerful density-dependent factor (BEGON et al. 1990). Again, in this case, the only report of extensive parasitism on

pied flycatchers (MERINO & POTTI 1995) mentions effects on the nestling survival and not the recruitment rate of the population as a whole.

A factor influencing populations at their wintering grounds is possible.It has been proposed (BAILLIE & PEACH 1992) that weather conditions in Sahel are strongly correlated with population changes in western Palearctic passerines. However, no periodic factor in the Sahel region is known to influence bird populations in a cyclical way.

The form of the Figures 2.6-2.7 implies that the spring population (which comprises all birds that return and "decide" to stay and breed in the Forest of Dean) is determined by two thresholds for the years 1948-1957, the upper at approximately 195 individuals and the lower at approximately 95 individuals. Then, fluctuations take place at a more restricted level. The return rate has been shown (WILLIAMS & RODWELL 1992, ROTH & JOHNSON 1993, CUADRADO & HASSELQUIST 1994) to play a major role in the population size of bird migrant species. As far as the pied flycatcher is concerned, the fact that such fluctuations are a characteristic of the spring population and are not confined to any of the groups comprising the breeders (natives, immigrants, residents) (STENNING et al. 1988) indicates that the regulating parameter affects the birds as a whole, probably after they have returned. The key to the pied flycatcher's establishment has often been reported (MARCHANT et al. 1990) to be the provision of nestboxes; therefore, it may be that the availability of the latter comprises the limiting factor for the specific population. Such availability may be controlled either through territoriality among intraspecific members of the guild or through interspecific competition from other hole-nesting species (e.g.tits, MARCHANT et al. 1990). If the latter is the case, trends in the population densities of other hole-nesting species in the Forest of Dean are expected to relate with the spring abundance of the pied flycatcher. As a conclusion, it is likely that the cyclic pattern appearing in this population is a demonstration of population regulation occuring via the availability of nest-sites for the potential breeders. It would be interesting to establish whether these oscillations are imposed by another hole-nesting, competing

species or they are a sign of a population which is much influenced by territoriality that comprises a limiting factor only after the population density overpasses certain levels.

It has been reported (MOSS & WATSON 1991) that certain population cycles exhibited by territorial birds are due to behavioural patterns of the species. The model assumes that kin selection enables the population to increase as a result of the establishment of new territories by male sons inside or close to the parental ones. This increase reaches a threshold level when territory size can not be further reduced ;it results in extreme aggressiveness between the individuals which consequently leads to spacing and population crash. This model does not explain adequately why this crash occurs gradually and not in a single breeding season , however, it provides a mechanism consistent with some natural phenomena and it is original in its assumption that population fluctuations would be driven primarily by male, and not female , birds (see also chapter 1).

It is thus speculated that a behavioural mechanism may give rise to the cyclic pattern in the pied flycatcher as well, (at least where the population is not exposed to harsh climatic conditions), for example at the core of its range (England, southern Finland). Male pied flycatchers are more philopatric than the females and are more likely to survive and breed again after a successful breeding season (HARVEY et al.1985).The breeding performance of both sexes improves with age and experience. As a result, individuals (esp. males) that bred successfully in one year are likely to survive and breed again in the following year and in the same area. Provided that the minimum size of the territory is not fixed (as it has been shown for some species, KLOMR 1972) and the trend of the increase does not change unpredictably, this would lead to an increase in breeding population density. As polygyny is mainly observed in populations of high density (VIROLAINEN 1982), it may provide the threshold mechanism that generates a gradual population decrease through reduction of the clutch size and, consequently, recruitment rate. Reduced clutch size is a characteristic of β-females mated with polyterritoral males and a parameter of poor

reproductive efficiency, which is shown to relate with greater breeding dispersal (HARVEY et al. 1985, VIROLAINEN 1982, ALATALO et al. 1982). Thus, the less successfully they reproduce, the more likely they are to migrate. Eventually, at low densities, polygyny is expected to be reduced, so the effect of a clutch size reduction is reversed. Even if polygyny does take place , the large size of the territoty enables more successful reproductive allocation (ALATALO et al. 1982), therefore, the clutch size is expected to increase.Conventional statistical tests are not expected to detect such differences because the correlation parameters are not clear-cut as the overall change in the population is an effect of two different processes, the return of the philopatric males (according to the degree of succesful reproduction in the previous year) and the establishment of territories (according to density).

However, there is limited evidence that polygyny is a common phenomenon in the particular flycatcher population in Gloucectershire. There are no data on the breeding ability of such males. Yet, it would be interesting to test whether even slight fluctuations in the number of polygynous males are directly correlated with breeding population changes, although they may also serve as a delayed density-dependent mechanism. Last but not least, it should not be expected that such a process is powerful enough to dominate every other factor that may impinge on the population; it is shown (Figures 2.9-2.12) that not all fluctuations are cyclic and, even if they are, they are not of the same extent. The more towards the periphery of its range the species is found, the more likely is to be influenced by stochastic factors and fluctuate randomly (see INTODUCTION of this chapter)

From Figures 2.7-2.8 it can be seen that the spring population size from 1958 onwards tends to stabilize at approximately 110 individuals (≈55 pairs). Is this the "optimal" breeding population size for the particular habitat and what might be the factors that control its fluctuations?It has been proposed that food affects several breeding parameters in the pied flycatcher including fledging weight, tarsus length and clutch size (LUNDBERG et al. 1981, ALATALO & LUNDBERG 1984, JARVINEN 1989). On the other hand, the species has been reported as a food generalist (BIBBY

& GREEN 1980, ATLEGRIM 1992, HAEMIG 1992) and oak forests as the Forest of Dean are its preferred habitat (LACK 1966, LUNDBERG et al. 1981, VILBASTE & ZEIVITS 1987), so it is not very probable that food may exert control on the specific popualtion. Another more likely factor is the availability of nest holes for breeding: if 55 pairs are considered the population in equilibrium, that leads to an estimation of 2.2 pairs/ha, a density which is towards the highest estimates given in the literature (LUNDBERG et al. 1981, ALATALO & LUNDBERG 1984). The pied flycatcher might not assess the availability of nestboxes the same way as humans do (that is, the percentage occupied by broods): a flycatcher may not be always able to distinguish between an unmated and a mated individual; a population of 110 birds plus 40% of single males and 40% unmated females (HARVEY et al. 1985) will then be perceived as 190 competitors! A more straightforward clue of the possible influence of the number of breeding adults on the breeding success is provided by k1 and k3 in years 1948-1954; then, the population size was much above 55 pairs and potential natality appeared reduced whereas mortality of hatchlings was increased.

Chapter 3:THE CASE OF THE CURLEW *Numenius arquata* : DOES HUNTING INFLUENCE WINTER SURVIVAL RATE ?

INTRODUCTION

In everyday life, disturbance is defined as the interruption of a settled state. In community ecology, disturbance is considered as every activity that leads to a removal of species and opening up of space (BEGON et al. 1990). Random "catastrophes" (e.g.. volcanic eruptions) and periodically anticipated "disasters" (e.g. hurricanes) seem to be major disturbance forces acting on a large scale. In most cases, however, it is difficult to decide whether an event truly acts as disturbance or whether is a participant in a condition of dynamic equilibrium.

Human disturbance has commonly been referred to as of fundamental importance in shaping the world's ecosystems. It is claimed that there is virtually no place on the Earth that has not been affected by the human presence. Nevertheless, the fact that humans are undeniably a part of the planet's ecosystems raises the question of whether humans play the role of one of several natural forces or act in an extreme manner causing perturbations that otherwise would not have been observed. Habitat alteration and loss, for example, is regarded as an expression of extensive human disturbance (DOLMAN & SUTHERLAND 1994) whereas hunting may be considered as a substitute for natural predation.

The claim that hunting by humans operates as a natural predation force has been one of two competing argument as far as the effect of shooting on populations is concerned: the compensatory mortality hypothesis states that if shooting reduces density to a certain threshold level, a compensatory reduction in mortality due to other factors will occur so that overall survival is unaffected. Such compensation is thought to take place either because at lower densities there is less competition for limited

resources (e.g. food and cover) or there is a decline in other density-dependent causes of mortality (i.e.predation). The security level ***c*** is estimated as **1-So** where **So** is the survival rate of the population in the absence of hunting ; it indicates that hunters causing mortality at or below the level ***c*** harvest individuals that would have died anyway owing to other reasons. In contrast, the additive mortality hypothesis suggests a direct negative relationship between hunting and survival rate, i.e. as hunting mortality increases, survival decreases correspondingly (REXSTAD 1992, ELLINSON 1991).

In reality, it is unlikely that hunting acts in a totally compensatory or totally additive way. For example, if a group of birds with a natural annual mortality rate of 30% is subjected to a shooting mortality rate of 10%, the additive mortality will not be 40%. This is because a fraction of the individuals harvested would have died anyhow of natural causes without shooting; this fraction is approximately equal to the product of the natural mortality rate and the shooting mortality rate or 3% in this example Thus, if additive mortality occured, total annual mortality would be 40%-3%=37%. On the other hand, the totally compensatory hypothesis requires that natural mortality below the threshold point ***c*** is perfectly density-dependent which is only rarely the rule. If natural mortality is partially density-dependent, there will be incomplete compensation and total annual mortality will lie between 30% and 37% in the above example.

To distinguish between additive and compensatory mortality, the following predictions are made (POLLOCK et al. 1994, REXSTAD 1992, ELLINSON 1991):

1. variations in survival rates are related to variations in shooting pressure

2. no effect of shooting on annual mortality (survival) rate up to a certain threshold of shooting mortality → **total compensatory mortality**

3. a positive relationship between non-hunting mortality and density, particularly between non-hunting mortality aftre shooting and post-shooting density. Density-

dependent mortality is also assumed in unhunted populations → **partial/total compensatory mortality**

4. response of survival rate estimates to variation in harvest regulations (e.g. daily bag limit, season length) → **additive mortality**

5. estimation of slope of linear relationship between survival rate and kill rate estimates →**additive/compensatory mortality (depending on the slope)**

In this chapter I shall test "prediction 1" for a population of marked curlews *Numenius arquata* that winter at the river Tees estuary, England and speculate on the additive or compensatory mortality acting on the particular population. Continuous data of sightings of individually colour-marked birds are available since 1976 and these years include the hunting period before 1981 and the non-hunting one after the Introduction of the Wildlife and Countryside Act in 1981. My aim is to check whether any variation in the survival rate between these groups of years might be attributed to hunting.

MATERIALS AND METHODS

the species: curlews (*Numenius arquata*) breed and winter in Britain in internationally important numbers. The breeding population of about 35.000 pairs is some 28% of the European total, whilst the 91.000 wintering birds represent 30% of the East Atlantic flyway size (BATTEN et al. 1990). Breeding curlews are associated with a variety of habitats from submontane grasslands to river valleys and lowland heather moors. Rough or overgrown damp pasture, clover and cereal crops also appear to be attractive as nesting sites (MARCHANT et al.1990). Although breeding populations are more numerous on upland meadows and lower moorland, the majority of the wintering birds (more than 50%, including the Tees population) is found on estuarines and coasts.

The species feeds on a wide range of medium-large invertebrates. On intertidal areas, curlews take most of the common bivalves, molluscs, polychaete worms and crustacea (e.g. *Carcinus*). Inland, adult and larvae insects -and especially earthworms- form the bulk of their diet (BATTEN et al.1990).

the habitat: The Tees estuary comprises an area of approximately 15 km^2 in north-east England (54° 37' N, 1° 12' W). It includes a main shipping channel and 3 intertidal areas (Seal Sands, North Gare Sands, Bran Sands). To the north-west and west of the estuary lie extensive areas of rough pasture and brine fields. There are two main feeding habitats for the curlews at the Tees estuary, the intertidal mudflats of which Seal Sands is the most productive (TOWNSEND 1981a) and the pastures and brine fields around them. The area is heavily industrialised and brine extraction operations take place at well-heads in the pastures adjacent to the estuary.

the analysis: curlews comprise one of the main shorebird species wintering in large numbers (500-1000 birds) at the Tees estuary. They have been studied on and around Teesmouth since 1976, particularly in relation to their use of the intertidal mudflats and the wet meadows and brine fields close to them. Over 300 individuals have been trapped with canon-netting and marked with unique combinations of colour rings. The population has been monitored continuously since 1976, throughout the year, at low and high water and across the whole area of the estuary. Observations of marked birds have been made with a 15-60x60 telescope or 10 x 50 binoculars and all reports of marked birds are stored on computer files. Curlews at the Tees estuary do not breed; they arrive towards the end of the summer from Fennoscandia and migrate back to their breeding grounds at the beginning of following spring (but some juveniles spend the summer at their wintering area). The observation year for the wintering population at the Teeside starts on the 1st of July and finishes on the 30th of June of the following calendar year. As spring departure dates of individually marked birds are confined almost entirely to the months of March and early April (EVANS 1988), birds that

disappeared between the 1st of July of year x and the 28/29th of February of year x+1 are considered as "winter losses", whereas ones that disappear between the 1st of March and the 30th of July of the same year are thought of as "summer loses".

For the estimation of annual adult survival rates, all available data on bird observations from 1976 to 1995 (February) have been used. For example, birds reported alive in one spring but not seen again until several springs (or winters) later are considered alive for all the intervening years. As the "autumn" period lasts, by definition, longer than the "spring" (autumn: July-February, spring: March-June, including months spent at the breeding grounds) birds are more likely to be directly observed in autumn. Thus, estimations of numbers that have actually survived to spring migration are usually indirect, from sightings of individuals in the subsequent years.

Possible sources of bias in such estimations are:

- the assumption that birds are always philopatric and feed regularly on the same areas. If some individuals tend to move away from the observation regions, then they are likely to be missed and considered dead while actually alive. Such misleading evidence results in exaggerated mortality. However, it is known (EVANS 1988) that the particular population at the Tees estuary exhibits a high degree of philopatry as almost no reports of curlews ringed at Teesmouth have been received from other British estuaries.

- the rate of succesful observation (estimated as % birds actually seen in the particular year of those known to be alive), as it varies according to the number and the experience of the observers and the meteorological conditions; the correct identification of an individual through a telescope or binoculars is difficult on wet or misty days when the colours of the rings are not distinguishable.

- practical misfortunes e.g.losses of rings or fading of colours. In some cases, it is easy to decide whether a colour report is a wrong one as it identifies a bird that is

definitely known as dead. However, as only few birds have been found dead, the possibility of validating the majority of the colour reports is very small.

- due to the nature of the observation, it is impossible to be absolutely sure of when and where exactly a bird has died , unless its corpse is found. For example, if a bird was last seen in October 1991, it is considered as an "autumn" loss although it may have escared observation until after the spring migration when it died. Also, a bird last seen in March is reported as a "spring" loss although it may well have died soon after it was observed and before its emigration. Such errors are inherent in the analysis and can not be avoided; nevertheless, it seems that they do not pose a serious bias in comparisons, as they are assumed to remain proportionally the same throughout the years.

A total of 359 curlews have been trapped and ringed since 1976 (data updated in February 1995) but not all of them were used in the analysis (table 3.1). The following categories were excluded:

- birds that have been seen only on the date of ringing and not afterwards, as it seems that the stress of capture may have led them to move away from the estuary, possibly temporarily, immediately after marking.

- birds that have appeared at the Teesmouth only in early autumn and (possibly) March. Such individuals are considered as "migrants" as they appear to use the estuary only for a short time. Hence, their losses are irrelevant to the question of mortality at the Teesmouth.

- birds that could not be sexed with confidence, either because they were juveniles when trapped (age category 3 or 5) or because their bill-length fell into the overlapping region of the bimodal size-frequency distribution of bill-lengths (fig.1).In agreement with TOWNSEND 1981a, the most clear-cut difference between the sexes in curlews is the length of the bill (males <127 mm, females>131 mm).

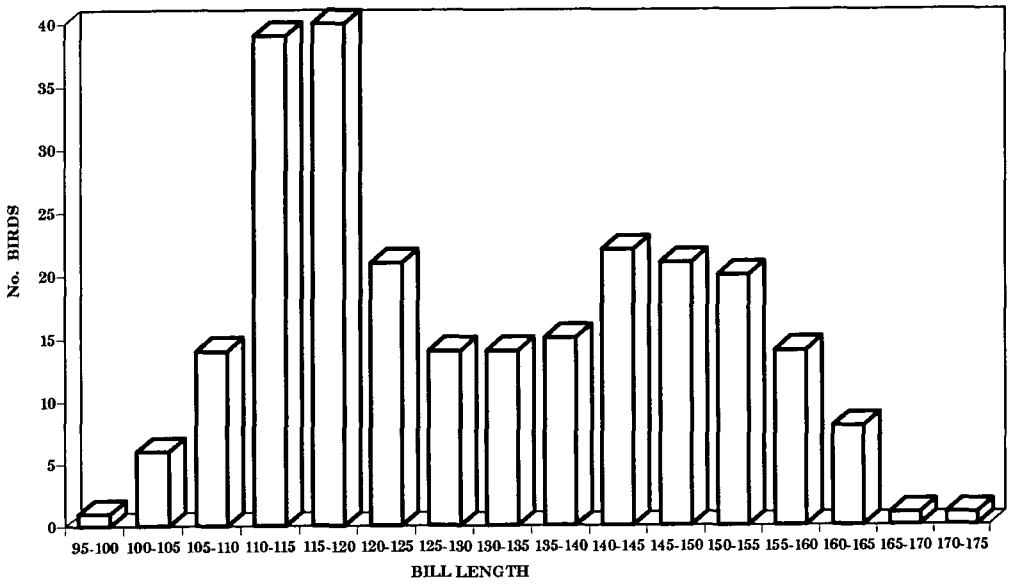
- birds that were marked in 1994, due to insufficiency of data

The statistical approach for the comparison of mean annual survival rates between different groups of years is the t-test for binomial distributions. Comparisons between male and female survival rates for the same period of time are performed with a 2x2 contigency table for binomial distributions as described in CAMPBELL 1989.

Table 3.1: Categories of curlews at the Tees estuary population

TOTAL NUMBER OF BIRDS COLOUR-RINGED UNTIL FEBRUARY 1995	359
BIRDS USED IN THE ANALYSIS	224 (127 males, 97 females)
MIGRANTS	28
BIRDS NOT SEEN AFTER RINGING	53
OF UNKNOWN SEX, JUVENILES	35
INSUFFICIENT / MISSING DATA	19

Figure 3.1: Bill-length frequency distribution in adult curlews captured at Teesmouth (1976-1994)



RESULTS

Annual winter survival was estimated separately for males and females and for each year (1976 to 1994) from the absolute numbers of individuals observed (or known to be) alive in autumn and/or the following spring (figures 3.2, 3.3, 3.4, 3.5 and APPENDIX II) Figures 3.2 and 3.4 present data for males and females respectively, for the years before shooting was banned and figures 3.3 and 3.5 the data for the years after the shooting ban.

Figure 3.2: Absolute numbers of male birds alive in years 1976-1982

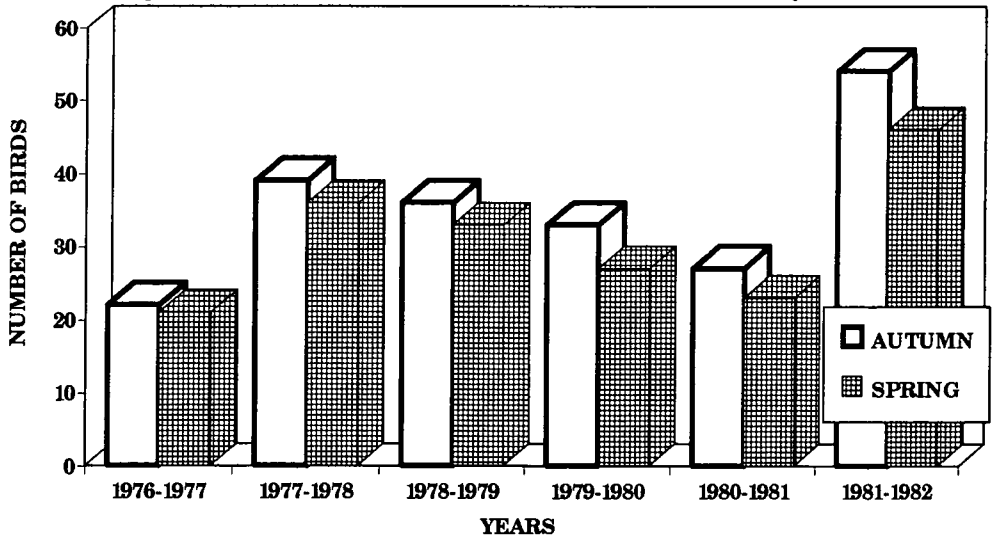


Figure 3.3: Absolute numbers of male birds alive in years 1982-1994

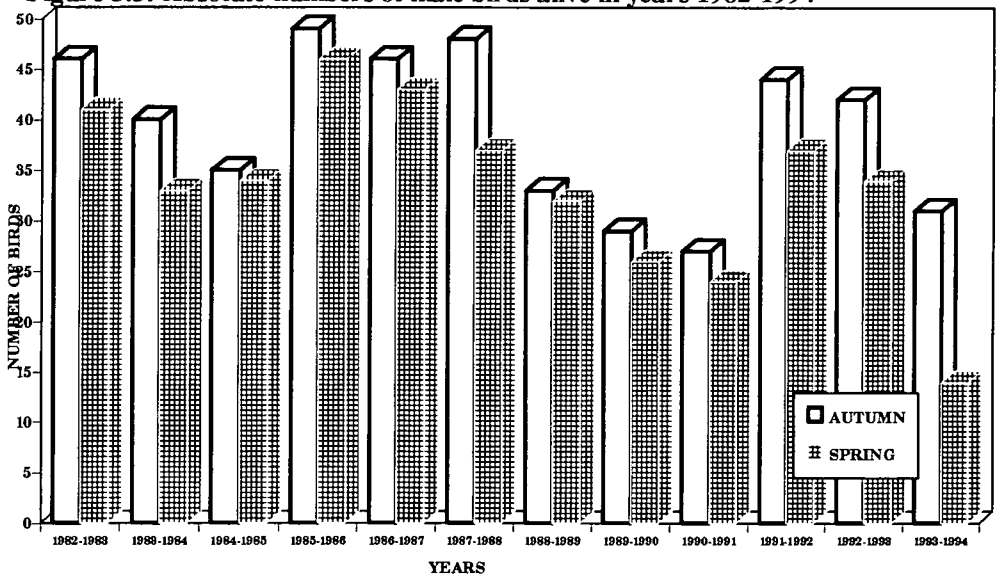


Figure 3.4: Absolute number of female birds alive in years 1976-1982

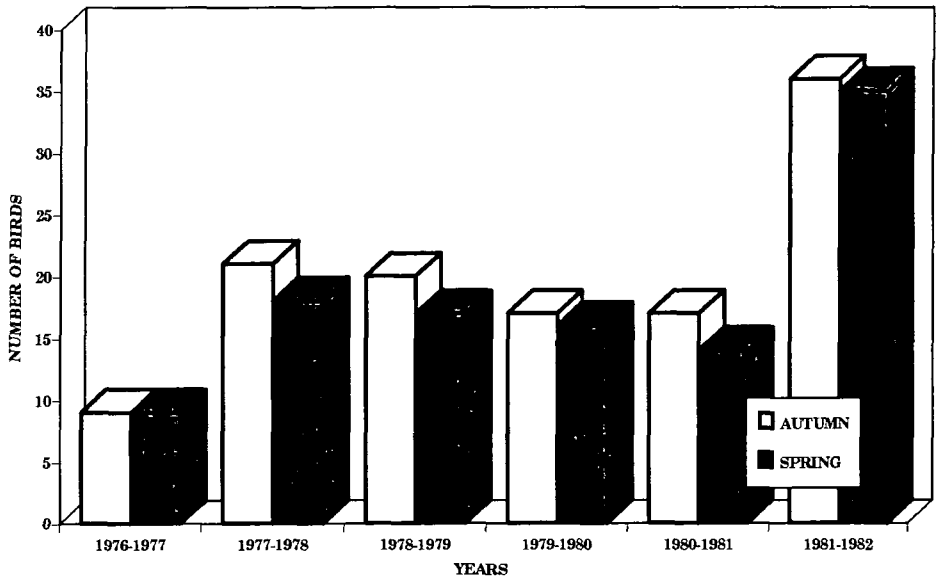
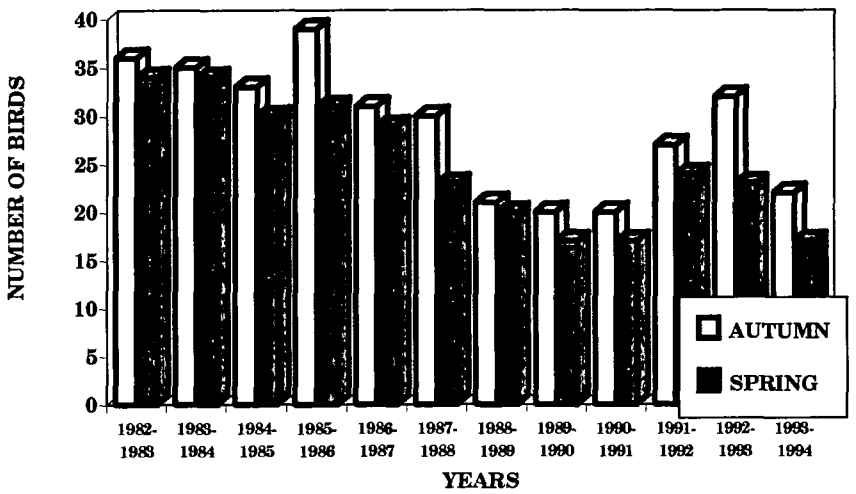


Figure 3.5: Absolute numbers of female birds alive in years 1982-1994



The fluctuations in time of the % overwinter survival (i.e.from autumn to 1st March) of male and female curlews are shown in figure 3 6:

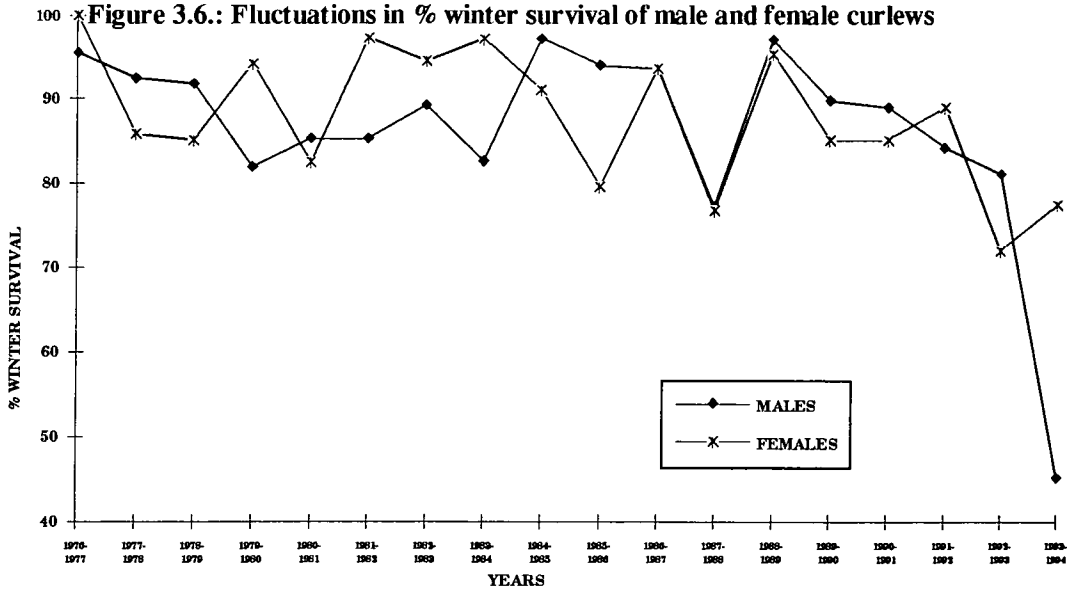


Figure 3.6.: Fluctuations in % winter survival of male and female curlews

For the purpose of the statistical analysis, years were grouped into 3 categories:

•1976-77 to 1981-82: this is the period of the time when hunting of curlews was permitted on the pastures and brine fields at the Tees estuary (but not on the intertidal areas which are in private ownership)

•1982-83 to 1993-94: this comprises the period after shooting of curlews was totally prevented

•1982-83 to 1988-1989: it was noticed that the apparent survival of the birds decreased substantially during the last years of the study (Figure 3.6). It was also estimated that, a high percentage of the total number of marked curlews had not been observed, while known to be alive, especially in recent years(Figure 3.7). An estimation (Figure 3.9) of the cumulative number of birds missed from observation for one or more years while alive showed that this number reached an asymptote after 5 years ,which means that, in realistic terms,if individuals are not observed after 5 years of disappearance, they are probably dead. As it is known that the degree of succesful observation varies from year to year (Figure 3. 8), it was assumed that if the last 5 years of the study were omitted from any calculations, the bias towards higher ranges

of winter mortality would be eliminated, as most of the birds will then have been allowed the critical period of 5 years before concluding that they are dead.

Figure 3.7: Absolute and % numbers of birds not seen while alive

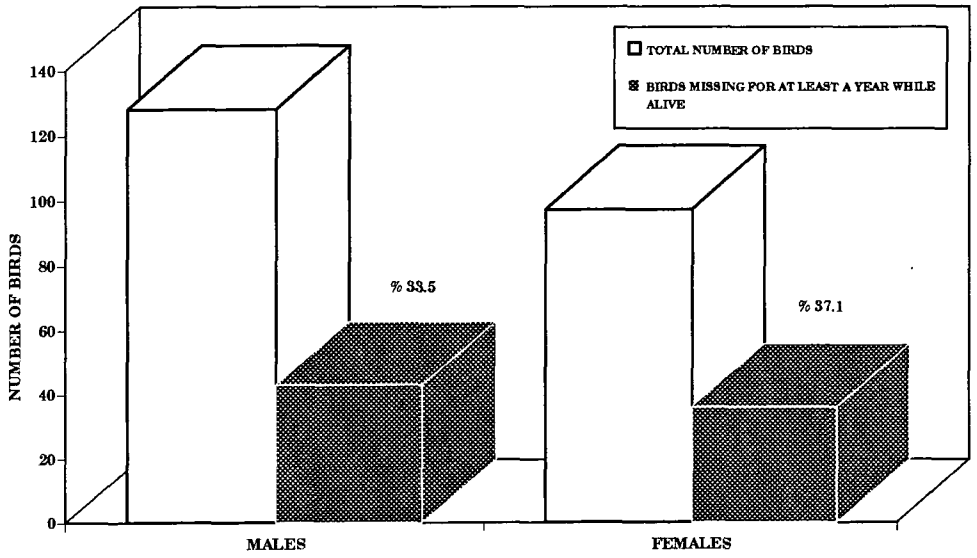


Figure 3.8: Fluctuations in % successful observation during the study

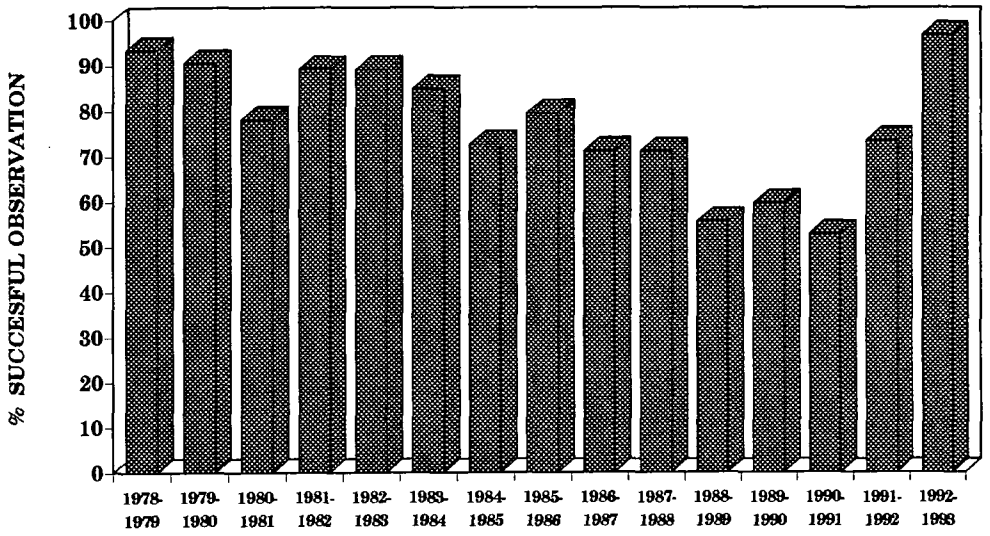
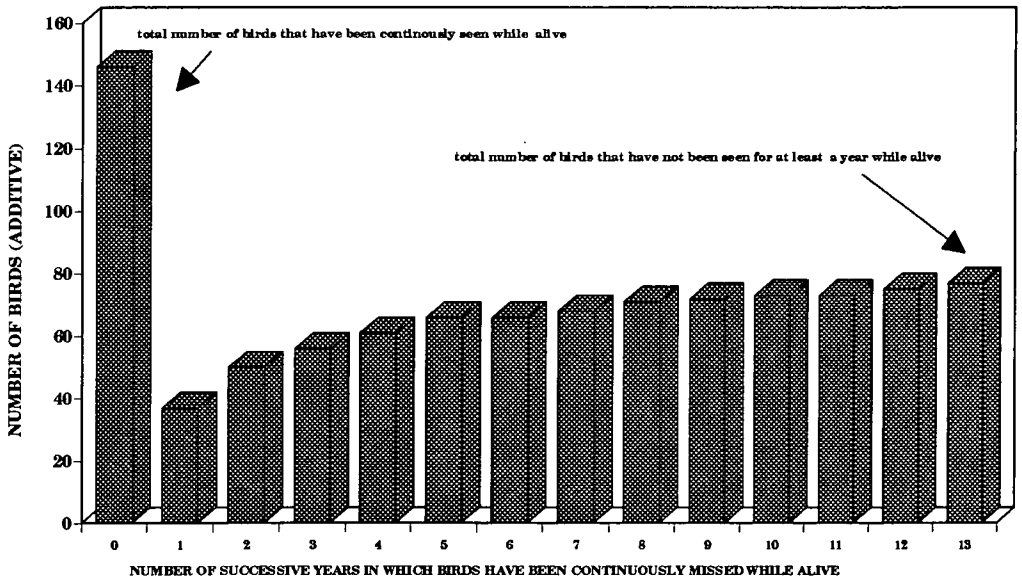


Figure 3.9: Cumulative number of birds missed from observation while alive (years 1976-1994)



The mean % winter survival rates for each group of years are shown in Table 3.2 and figures 3.9,3.10 & 3.11:

Table 3.2 :Mean % winter survival of curlews at the Tees estuary

	MALES	S.Error	FEMALES	S.Error	SUM	S.Error
1976-1982	88.15	2.2	90.83	2.6	89.1	1.7
1982-1989	89.56	1.7	89.33	2	89.4	1.3
1982-1994	85.31	1.6	86.41	1.8	85.7	1.2

The results of the t-test show that the null hypothesis of no difference in % winter survival between different groups of years for both sexes pooled and for each sex separately can not be rejected. Also the X^2-test comparing values for each sex and for the same period gives non-significant results. It is, however, interesting that the difference in the survival rates between the years 1982-1989 and 1982-1994 is marginally larger than the difference between either of them and the period before 1981. In addition, even though the results are not statistically significant, it is worth mentioning that the trend of the survival rate might turn out completely different in accordance with the group of years that are actually involved in the analysis. Hence,the survival rate for the whole population remains almost the same before and after the shooting ban if only data until 1989 are considered; it shows a 4% decrease if the last 5 years of survey are included. The winter survival rate of male curlews appears 3% reduced after 1982 if all data are used in the calculations, whereas it shows a 1% increase if the last 5 years of assumed observation bias are excluded ! Similar results are also observed with the data for the female curlews whose mortality in the non-hunting period is 3% exaggerated if years after1989 are noted .

Figure 3.10: % survival of male and female birds (1976-1994)

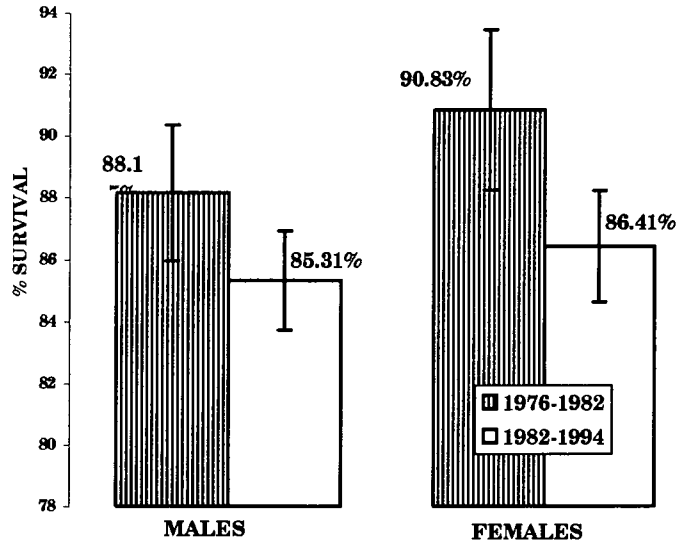
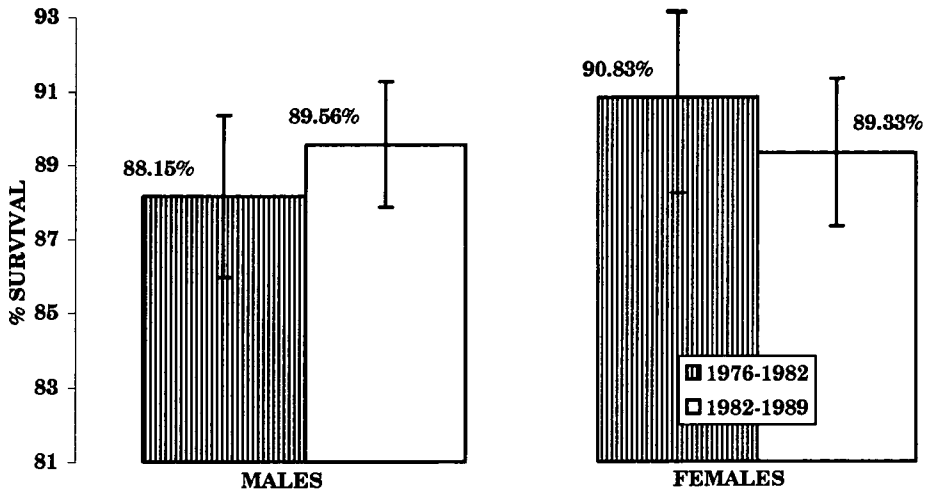


Figure 3.11: % survival of male and female birds (1976-1989)



DISCUSSION

The present analysis of data from the Tees estuary curlew population shows that there is no variation in the winter survival rate of the birds between the hunting (1976-1981) and the non-hunting (1982-1994) period or between the sexes. In this particular case, values of survival are chiefly influenced by whether years of presumed observation bias are included in the analysis and not by whether they are calculated

before or after the hunting ban. It appears that the marginal (but not statistically significant) reduction in the survival rate of the curlews after 1982 is an effect of overestimated mortality due to birds that have been missed from observation while alive. It is, therefore, expected that, unless the dynamics of the population change dramatically or the degree of succesful observation falls substantially, future estimations of winter survival for the same popularion and for the same years will show an increase. Apparently, this is the reason mortality rates calculated in the past for the same periods and population (EVANS 1988) are 2-3% higher.

One might argue that the statistical test employed is of low power and a more appropriate test would possibly trace differences in survival rates in the years before and after 1982. and, thus, provide evidence favoring the additive mortality hypothesis for this curlew population. Such an argument is justified; the fact that hunting is not shown to cause additive mortality does not always lead to a compensatory mechanism. If the additive mortality losses are relatively small compared to the ones due to natural factors, it is difficult to disentagle them from random variation in natural mortality rates. In such cases there is poor correlation between population success and shooting intensity (LINDEN 1991). Moreover, no compensatory mortality can be envisaged unless there is a demographic, density-dependent factor to which it is closely related. For example, if spacing behaviour limits breeding density as in the Red Grouse (ELLINSON 1991), removal of established residents owing to shooting may permit non-breeders to breed. Sometimes, however, apparent compensation is not due to relaxation of density-dependent factors and, thus, the enhancement of the survival of the remaining birds;on the contrary, it is a result of immigration of individuals that would otherwise have survived elsewhere. The hypothesis of compensatory mortality is most applicable to populations prone to density-dependent control. Populations of high survival rate are unlikely to exhibit it (ELLINSON 1991).

Curlews are, in fact, one of these species whose annual survival is comparatively high even though they have to undertake long migrations to and from their breeding areas. The greater part of the annual mortality occurs, however, in the wintering areas and , even there, it is comparatively low (EVANS 1981). The causes of natural mortality during winter have not been specified but it seems that they are not related to demographic factors. The rate at which birds can feed depends in part on the density of the prey and the proportion that is available at any moment. This availability has been mainly assessed in relation to the foraging technique employed and only rarely to the presence and numbers of the predators themselves.

In some cases (GOSS-CUSTARD et al. 1991), the density of curlews present on an estuary has been correlated with prey density, although it is not known whether such a relationship would lead to intraspecific competition above a certain threshold of predators. In manipulated experiments (ZWARTS & WANINK 1984) depletion of the prey and interference among curlews and oystercatchers (*Haematopus ostralegus*) has been observed, but it is unlikely that this occurs in natural conditions as the size and the number of the prey consumed by each of the species differ spatially and temporally. Last but not least, it is known (TOWNSEND 1981a) that some individual curlews establish territories on the mudflats of the Tees estuary which they actively defend. Because territoriality can occasionally be a strong demographic factor, it may be proposed that this is the way compensatory mortality acts on the Tees curlew population. Still, it seems improbable that this is the case; territories on the mudflats are defended by only a few birds and often only temporarily. For the non-breeding curlews, territoriality seems to be a choice of the individual, dependent on temporarily-acting factors. Thus, it is not the extensive phenomenon which is reported on their breeding grounds,associated with a particular population and habitat and often related to density and reproductive success (BERG 1994, 1993, 1992a, 1992

Consequently, despite the lack of significant variation in survival rates between the hunting and non-hunting period, it appears that there is little evidence towards the hypothesis of compensatory mortality in the particular curlew population as no demographic mechanism strongly related to it has been detected. If the rate of the hunting mortality is approximately 2% (as estimated in EVANS 1988), then it coincides with the standard error of mean winter survival rate for the years before and after hunting prohibition (Table 3.2) so it is unlikely to be considered significant by a conventional statistical test. A hunting mortality of 2% is much lower that that reported for curlews from other European countries (MELTOFTE 1986) and it agrees with other modest estimations of general shooting mortality in Britain (McCULLOCH et al. 1992). Hunting pressure, however, may vary according to the migration patterns and the geographical areas occupied by each population (FRANCIS & COOKE 1992a,b REXSTAD & ANDERSON 1992). Thus, a comparatively low hunting pressure on a specific curlew population does not imply *a priori* that other populations of the species will be also slightly affected.

During hunting, differential mortality between the sexes may be attributed either to behavioural or physiological differences (e.g.in the timing of migration in relation to the post-nuptial molt). If survival in one of the sexes is lower, perhaps due to natural mortality, fewer birds are there to be reported, so the hunting mortality of this sex appears reduced. Differences in recovery rate occur when one sex is more likely to be shot and reported than the other (FRANCIS & COOKE 1992b). The latter has been suggested (EVANS 1988) to be the case for the curlews at the Tees estuary: it appears that feeding on the mudflats, at least for short-billed (male) curlews becomes progressively more difficult as the temperature falls during winter and the main prey *Nereis diversicolor* lie deeper in their burrows. As a result, males move to the adjacent pastures and brinefields where the availability of earthworms in the thin surface layer of the soil remains adequate for the birds to meet their energy requirements

(TOWNSEND 1981b). Birds (mainly males) feeding on these fields before 1982 were more likely to be shot as shooting was permitted only there and not in the intertidal areas. In fact, the slightly lower (but not statistically significant) winter survival before 1982 in males compared to females provides some evidence of differential mortality between the sexes.

In conclusion, despite the lack of variation in survival rates before and after hunting (see INTRODUCTION, prediction"1"), the hypothesis of compensatory hunting mortality acting on the Tees estuary curlew population seems unlikely as there is no evidence of a demographic mechanism related to it. The hypothesis of additive hunting mortality seems probable , although it must be restricted to low levels, undetected by a conventional statistical test. Female and male winter survival do not show parallel fluctuations, but they appear comparatively stable in time, except in the last 5 years of the study when the corresponding reduction is attributed to observation bias.

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SUMMARY

Population processes are investigated in two migratory bird species, the pied flycatcher (*Ficedula hypoleuca*) and the curlew (*Numenius arquata*). Key-factor analysis is applied on long-term data (1948-1968) from a population of pied flycatchers in southern England; no extensive density-dependence is detected. The key-factor is shown to be mortality (or emigration) outside the breeding season and it is strongly correlated with changes in breeding population density that occur in a cyclic way. It is speculated that a behavioural mechanism may exist behind such a pattern.

Long-term observation data (1976-1994) on curlews wintering at Teesmouth, south-eastern England, are assessed in order to compare winter survival rates in the population before and after the shooting ban in 1982. No difference in survival rates is detected, either when both sexes are considered together or separately, however, the hypothesis of compensatory mortality is abandoned as there is no evidence for a demographic mechanism related to it. The effects of using biased data are also discussed.

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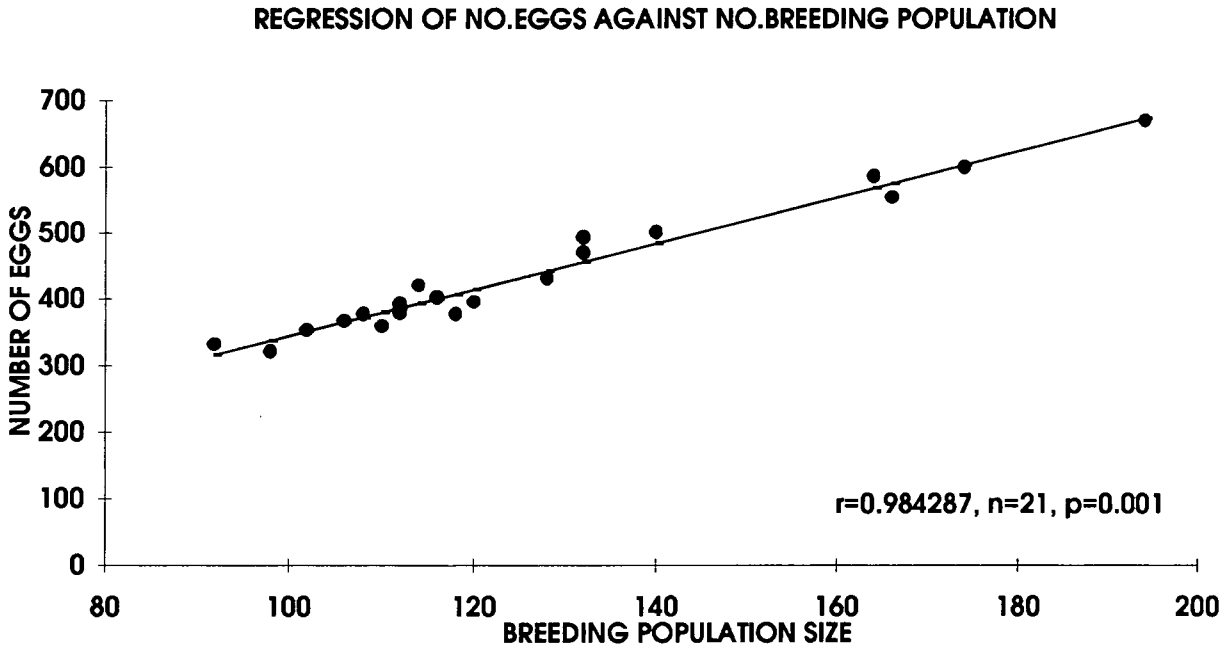
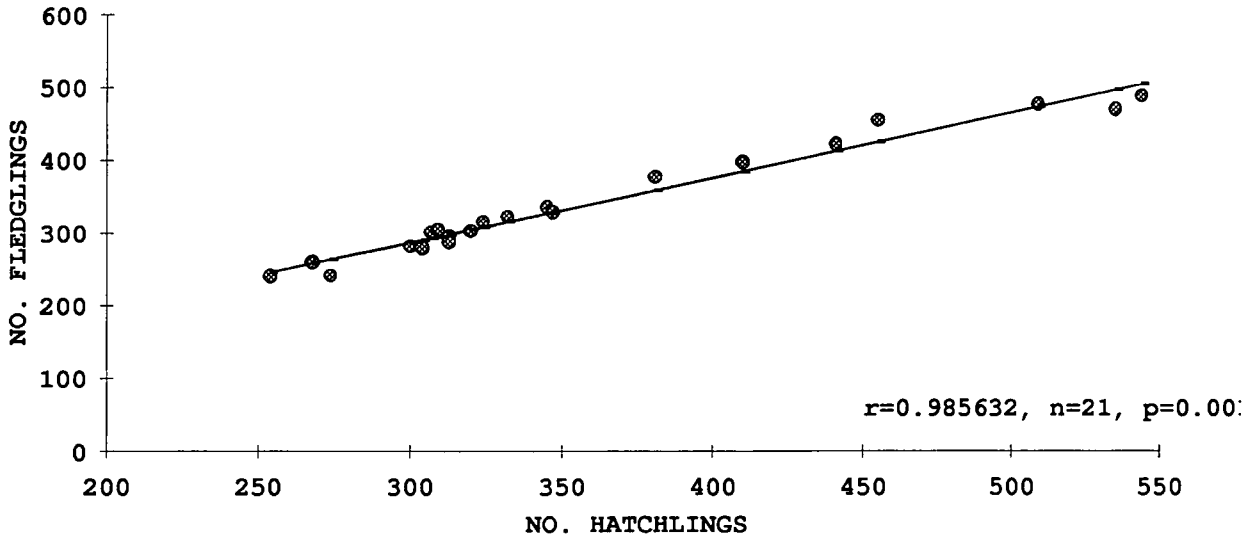
APPENDIX I

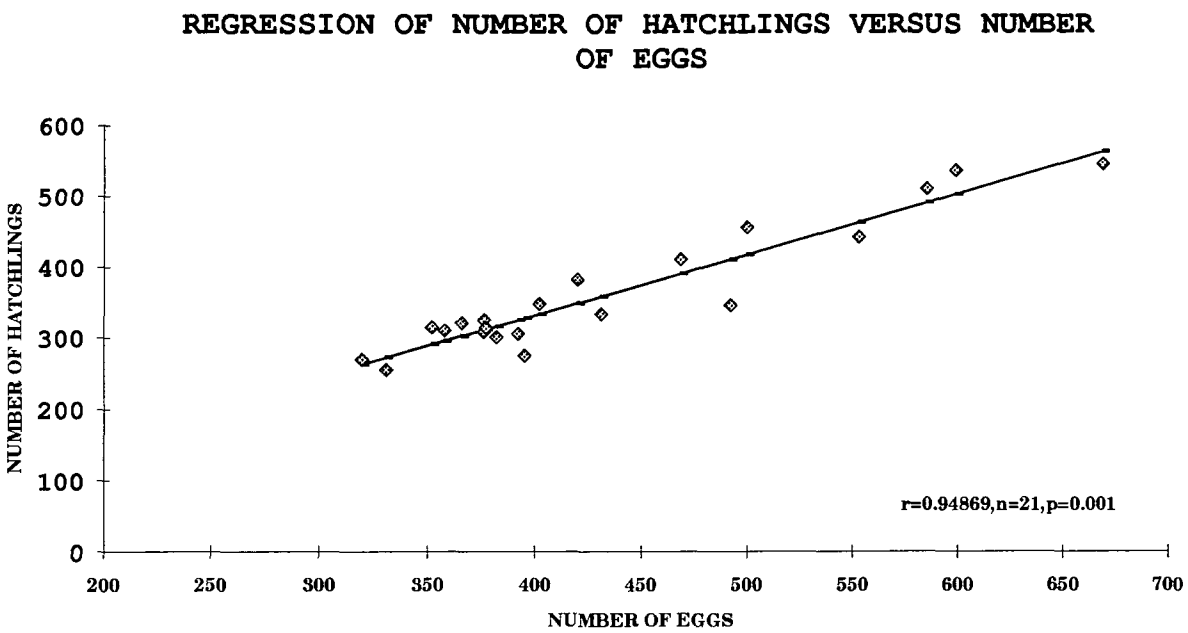
			k-values (MODE LAYIND DATE)			
		K1	**K2**	**K3**	**K4**	**KT**
	1948	0.107515	0.032936	0.004409	0.586996	0.731856
	1949	0.103541	0.116666	0.010132	0.501994	0.732333
	1950	0.118513	0.046467	0.021835	0.580964	0.767779
	1951	0.130521	0.037533	0.042435	0.542145	0.752634
	1952	0.129942	0.067954	0.034909	0.619998	0.852804
	1953	0.14153	0.07354	0.014551	0.638489	0.86811
	1954	0.118099	0.031663	0.000731	0.728835	0.879328
	1955	0.156306	0.065338	0.007213	0.675347	0.904204
	1956	0.129696	0.039008	0.020353	0.693268	0.882324
	1957	0.115599	0.087264	0.019248	0.479309	0.70142
	1958	0.119851	0.044875	0.011365	0.653966	0.830057
	1959	0.137949	0.084654	0.010511	0.654932	0.888047
	1960	0.133642	0.07883	0.021611	0.539912	0.773995
	1961	0.145525	0.116311	0.039194	0.537369	0.838399
	1962	0.124939	0.083337	0.028029	0.606967	0.843272
	1963	0.149298	0.048032	0.006264	0.619133	0.822727
	1964	0.129515	0.044532	0.018749	0.588017	0.780814
	1965	0.133713	0.060673	0.003982	0.514737	0.713105
	1966	0.134699	0.046306	0.026604	0.562387	0.769996
	1967	0.12833	0.048849	0.019478	0.599291	0.795948
	1968	0.150785	0.07692	0.018357	0.736187	0.982249
			K VALUES (MEAN LAYING DATE)			
		K1	**K2**	**K3**	**K4**	**KT**
	1948	0.107515	0.032936	0.004409	0.586996	0.731856
	1949	0.103541	0.116666	0.010132	0.501994	0.732333
	1950	0.118513	0.046467	0.021835	0.580964	0.767779
	1951	0.130521	0.037533	0.042435	0.542145	0.752634
	1952	0.129942	0.067954	0.034909	0.619998	0.852804
	1953	0.14153	0.07354	0.014551	0.638489	0.86811
	1954	0.118099	0.031663	0.000731	0.728835	0.879328
	1955	0.156306	0.065338	0.007213	0.675347	0.904204
	1956	0.129696	0.039008	0.020353	0.693268	0.882324
	1957	0.115599	0.087264	0.019248	0.479309	0.70142
	1958	0.119851	0.044875	0.011365	0.653966	0.830057
	1959	0.137949	0.084654	0.010511	0.654932	0.888047
	1960	0.133642	0.07883	0.021611	0.539912	0.773995
	1961	0.145525	0.116311	0.039194	0.537369	0.838399
	1962	0.124939	0.083337	0.028029	0.606967	0.843272
	1963	0.149298	0.048032	0.006264	0.619133	0.822727
	1964	0.129515	0.044532	0.018749	0.595986	0.788783
	1965	0.12673	0.049362	0.010171	0.611647	0.79791
	1966	0.13806	0.06092	0.028506	0.5983	0.825786
	1967	0.128279	0.048749	0.019177	0.679947	0.876152
	1968	0.148201	0.057695	0.012031	0.672518	0.890445

		PIED FLYCATCHER DATA, 1948-1968					
for the years 1965-1968, normal broods are estimated according to the mean laying date							
		NORMAL BROODS (N)	2N	NO EGGS	no. hatche	no.fledg	sum.pop.
	1948	57		420	381	376	510
	1949	66	132	492	345	334	521
	1950	82	164	585	509	476	663
	1951	87	174	599	535	469	676
	1952	97	194	669	544	487	692
	1953	83	166	553	441	421	609
	1954	70	140	500	455	454	632
	1955	59	118	376	307	300	483
	1956	51	102	352	313	294	454
	1957	46	92	331	254	239	398
	1958	66	132	469	410	396	577
	1959	64	128	431	332	321	506
	1960	56	112	382	300	280	416
	1961	60	120	395	274	240	386
	1962	56	112	392	304	278	445
	1963	55	110	358	309	303	441
	1964	53	106	366	320	302	426
	1965	54	108	376	324	314	458
	1966	56	112	377	313	286	460
	1967	58	116	402	347	327	469
	1968	49	98	320	268	258	414
for the years 1965-1968, normal broods are estimated according to the modal laying date							
		NORMAL BROODS	NO EGGS	no. hatchec	no.fledg	summer population	
	1948	57	420	381	376	510	
	1949	66	492	345	334	521	
	1950	82	585	509	476	663	
	1951	87	599	535	469	676	
	1952	97	669	544	487	692	
	1953	83	553	441	421	609	
	1954	70	500	455	454	632	
	1955	59	376	307	300	483	
	1956	51	352	313	294	454	
	1957	46	331	254	239	398	
	1958	66	469	410	396	577	
	1959	64	431	332	321	506	
	1960	56	382	300	280	416	
	1961	60	395	274	240	386	
	1962	56	392	304	278	445	
	1963	55	358	309	303	441	
	1964	53	366	320	302	426	
	1965	55	364	312	308	458	
	1966	47	320	278	256	460	
	1967	58	402	347	327	469	
	1968	50	327	269	259	414	


REGRESSION OF NO.EGGS AGAINST NO.BREEDING POPULATION
NUMBER OF EGGS
700
600
500
400
300
200
100
0
80
100
120
140
160
180
200
BREEDING POPULATION SIZE
r=0.984287, n=21, p=0.001

REGRESSION OF THE NUMBER OF FLEDGLINGS AGAINST THE NUMBER OF HATCHLINGS




REGRESSION OF NUMBER OF HATCHLINGS VERSUS NUMBER OF EGGS
NUMBER OF HATCHLINGS
600
500
400
300
200
100
0
200
250
300
350
400
450
500
550
600
650
700
NUMBER OF EGGS
r=0.94869,n=21,p=0.001

APPENDIX II

% winter survival of curlews at the Tees estuary, 1976-1994

	autumn	spring	
	MALES	MALES	% survival
1976-1977	22	21	95.45454545
1977-1978	39	36	92.30769231
1978-1979	36	33	91.66666667
1979-1980	33	27	81.81818182
1980-1981	27	23	85.18518519
1981-1982	54	46	85.18518519
1982-1983	46	41	89.13043478
1983-1984	40	33	82.5
1984-1985	35	34	97.14285714
1985-1986	49	46	93.87755102
1986-1987	46	43	93.47826087
1987-1988	48	37	77.08333333
1988-1989	33	32	96.96969697
1989-1990	29	26	89.65517241
1990-1991	27	24	88.88888889
1991-1992	44	37	84.09090909
1992-1993	42	34	80.95238095
1993-1994	31	14	45.16129032

	autumn	spring	
	FEMALES	FEMALES	% survival
1976-1977	9	9	100
1977-1978	21	18	85.71428571
1978-1979	20	17	85
1979-1980	17	16	94.11764706
1980-1981	17	14	82.35294118
1981-1982	36	35	97.22222222
1982-1983	36	34	94.44444444
1983-1984	35	34	97.14285714
1984-1985	33	30	90.90909091
1985-1986	39	31	79.48717949
1986-1987	31	29	93.5483871
1987-1988	30	23	76.66666667
1988-1989	21	20	95.23809524
1989-1990	20	17	85
1990-1991	20	17	85
1991-1992	27	24	88.88888889
1992-1993	32	23	71.875
1993-1994	22	17	77.27272727

		autumn	spring			
		sum	sum	% survival		
	1976-1977	31	30	96.77419355		
	1977-1978	60	54	90		
	1978-1979	56	50	89.28571429		
	1979-1980	50	43	86		
	1980-1981	44	37	84.09090909		
	1981-1982	90	81	90		
	1982-1983	82	75	91.46341463		
	1983-1984	75	67	89.33333333		
	1984-1985	68	64	94.11764706		
	1985-1986	88	77	87.5		
	1986-1987	77	72	93.50649351		
	1987-1988	78	60	76.92307692		
	1988-1989	54	52	96.2962963		
	1989-1990	49	43	87.75510204		
	1990-1991	47	41	87.23404255		
	1991-1992	71	61	85.91549296		
	1992-1993	74	57	77.02702703		
	1993-1994	53	31	58.49056604		
the 1st and the 2nd column represent number of individual marked birds which were observed						
(or known to be alive) in the particular year and season						

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